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X

Notice of the Retirement of Dr. John N. Couch as Chairman of the Editorial Board of the Elisha Mitchell Scientific Society

After sixteen years as Editor of the *Journal of the Elisha Mitchell Scientific Society*, Professor John N. Couch has asked to be relieved of this responsibility. He will devote his full time to his duties as Kenan Professor of Botany at the University of North Carolina.

At the Annual Business Meeting for 1960, the members of the Society extended to Professor Couch a rising vote of thanks for the many years of skilled, distinguished, and unselfish service as Editor of the *Journal of the Elisha Mitchell Scientific Society*.

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The Psammophytes of the Carolina Fall-line Sandhills[1]

JAMES A. DUKE
Missouri Botanical Gardens, 2315 Tower Grove, St. Louis, Mo.

The fall-line hills are a discontinuous belt of rolling hills, floristically bizarre, extending from central North Carolina through central Alabama, locally to eastern Mississippi. This belt is generally from twenty to forty miles wide, with its inner margin at the fall-line. It is an area where streams, passing from the hard crystalline bedrocks of the piedmont to the soft sedimentary rocks of the coastal plain, undergo a comparatively rapid descent and often form waterfalls. Frequently the fall-line hills are divisible into two belts. The inner portion next to the piedmont, characterized by whitish or yellowish surface soils usually overlying a Cretaceous outcrop, is called the fall-line sandhills. An outer portion of the fall-line hills is often distinguishable and is called the red hills, characterized by red or orange sandy loams largely overlying post-Cretaceous outcrops.

The xeric sandhills, in a land of adequate rainfall, once supported vast areas of longleaf pine (Wells & Shunk, 1931). Unfortunately the pine forests have been decimated by the lumbering and turpentine industries and largely replaced by an essentially valueless growth of scrubby oaks. The current reforestation practice is to uproot and remove the oaks and to plant pines in their stead. The rigorous means of scarification may jeopardize the continued existence of such rare species as *Chrysoma pauciflosculosa* Greene and *Psoralea canescens* Michx.

The flora, often called simply the sandhill flora, is by no means confined to the fall-line sandhills. It occurs in several ecologically similar habitats of diverse geological origins, but it is probable that the fall-line sandhills were the first of these habitats available to plants after the Cretaceous inundation. Among more recently evolved niches which support similar floras are fluvial terraces, well-drained marine terraces, Pleistocene marine escarpments and emerged bars, old dunes, and recent dunes protected from salt spray.

The purpose of this study has been to enumerate the xerophytic elements of the sandhill flora and to analyze various geologic, geographic, and ecologic aspects of the flora as a whole. Species collected in the xeric sands of the fall-line sandhills during this study are recorded in Table I. For comparative purposes, younger sand ridges of Wayne County and Gates County in North Carolina and Nansemond County in Virginia are also included in the tabulation.

Pedology

The soils of the fall-line sandhills in the Carolinas are largely of two types, the Norfolk and the Orangeburg. In general, the Norfolk is prevalent in North Carolina, being partially supplanted south of the Santee River in South Carolina by the Orangeburg. The areal relations of the two sandhill soil types are well illustrated in the *Atlas of American Agriculture* (U.S.D.A., 1936).

A normal profile of the Norfolk soil consists of an organic-stained, gray sandy A_1 of a few inches' depth, sometimes overlain by a layer of white or yellow sand, the result of recent aeolian or pluvial activity; and A_2, one to three feet, of pale yellow sand; a B horizon, usually more than three feet deep, of yellow or faintly reddish-yellow friable sandy clay; and a C horizon of a mottled red, yellow, and gray sandy clay (U.S.D.A., 1936).

The Orangeburg soil has a red B horizon and may have a reddish A horizon. It is similar to the Norfolk in friability and in general lack of structure. It is reputedly derived from impure limestone (U.S.D.A., 1936), but its occurrence in

[1] Condensed from a dissertation, under the direction of Dr. A. E. Radford, submitted to the faculty of the University of North Carolina in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Botany, Chapel Hill, N. C.

Table I

Species collected, duration (a, annual; b, biennial; p, perennial; v, various), counties in which collected, northeastern limits

SPECIES	DURATION	Richmond Co., Ga.	Aiken Co., S. C.	Lexington Co., S. C.	Richland Co., S. C.	Kershaw Co., S. C.	Darlington Co., S. C.	Chesterfield Co., S. C.	Marlboro Co., S. C.	Scotland Co., N. C.	Richmond Co., N. C.	Moore Co., N. C.	Hoke Co., N. C.	Cumberland Co., N. C.	Harnett Co., N. C.	Wayne Co., N. C.	Gates Co., N. C.	Nansemond Co., N. C.	NORTHEASTERN LIMIT
Selaginella arenicola Underw.	p			•	•	•													N. C.
Pteridium aquilinum (L.) Kuhn	p	•	•	•			•				•								Nfld.
Juniperus virginiana L.	p			•															Can.
Pinus virginiana Mill.	p		•																N. Y.
Pinus australis Michx. f.	p	•	•		•		•								•	•		•	Va.
Pinus taeda L.	p		•				•											•	N. J.
Myrica pusilla Raf.	p																•	•	Del.
Carya glabra (Mill.) Sweet	p																•	•	Can.
Carya tomentosa Nutt.	p											•							Can.
Castanea pumila (L.) Mill.	p																•	•	Mass.
Quercus phellos L.	p	•																	N. Y.
Quercus falcata Michx.	p																•	•	N. Y.
Quercus incana Bartr.	p	•	•	•	•		•	•	•	•		•	•	•	•	•	•	•	Va.
Quercus laevis Walt.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Va.
Quercus marilandica Muenchh.	p	•	•	•			•	•		•		•	•	•		•			N. Y.
Quercus nigra L.	p	•				•		•		•					•				Del.
Quercus stellata Wang.	p	•	•									•			•				Mass.
Quercus stellata var. *margaretta* (Ashe) Sarg.	p		•	•		•					•	•		•		•	•	•	Mass.
Quercus laevis x nigra	p				•														Va.
Quercus incana x nigra	p																	•	Va.
Polygonum aviculare L.	a	•																	Nfld.
Polygonum convolvulus L.	a			•															Can.
Polygonum pennsylvanicum L.	a							•											N. S.
Eriogonum tomentosum Michx.	p	•	•	•	•			•											S.C.
Rumex hastatulus Baldw.	p	•	•	•				•											Mass.
Rumex acetosella L.	p															•			Can.
Polygonella polygama (Vent.) Gray	p		•	•	•	•	•										•		Va.
Polygonella croomii Chapm.	p				•			•											S. C.
Cycloloma atriplicifolium (Spreng.) Coult.	a		•	•		•													Can.
Chenopodium album L.	a		•			•								•					Can.
Chenopodium ambrosioides L.	v			•															Can.
Froelichia floridana (Nutt.) Moq.	a	•	•	•	•	•		•		•	•			•					Del.
Froelichia gracilis (Hook.) Moq.	a	•	•			•									•				N. Y.
Amaranthus hybridus L.	a			•															N. E.
Boerhaavia erecta L.	a		•																S. C.
Phytolacca americana L.	p			•		•		•								•	•		Can.
Portulaca oleracea L.	a									•									ME.
Mollugo verticillata L.	a	•		•			•	•		•									Can.
Stipulicida setacea Michx.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		N. C.
Siphonychia americana (Nutt.) T. & G.	p	•																	S. C.
Arenaria caroliniana Walt.	p	•	•	•		•		•	•	•	•	•	•	•	•				R. I.
Agrostemma githago L.	a		•																Can.
Silene antirrhina L.	a	•	•																Can.
Sassafras albidum (Nutt.) Nees	p	•	•	•		•				•	•	•				•	•	•	Me.
Warea cuneifolia (Muhl.) Nutt.	a	•		•	•	•		•											N. C.
Cardamine pennsylvanica Muhl.	p											•							Lab.

Table I—Continued

SPECIES	DURATION	Richmond Co., Ga.	Aiken Co., S. C.	Lexington Co., S. C.	Richland Co., S. C.	Kershaw Co., S. C.	Darlington Co., S. C.	Chesterfield Co., S. C.	Marlboro Co., S. C.	Scotland Co., N. C.	Richmond Co., N. C.	Moore Co., N. C.	Hoke Co., N. C.	Cumberland Co., N. C.	Harnett Co., N. C.	Wayne Co., N. C.	Gates Co., N. C.	Nansemond Co., N. C.	NORTHEASTERN LIMIT
Lepidium virginicum L.	a									•									Can.
Raphanus raphanistrum L.	a														•				Nfld.
Hamamelis virginiana L.	p																•		N. S.
Crataegus flava Ait.	p	•	•	•	•						•	•				•			Va.
Crataegus margaretta Ashe	p	•	•			•	•					•			•	•			Can.
Crataegus uniflora Muenchh.	p	•	•	•	•				•					•					N. Y.
Potentilla recta L.	p									•									Nfld.
Prunus angustifolia Marsh.	p	•	•																N. J.
Prunus caroliniana Ait.	p		•	•															N. C.
Prunus umbellata Ell.	p							•											S. C.
Prunus serotina Ehrh.	p	•																	N. S.
Amelanchier arborea (Michx. f.) Fern.?	p																•		Can.
Aronia arbutifolia (L.) Ell.	p														•				N. S.
Rubus flagellaris Willd.	p														•				Can.
Rubus cuneifolius Pursh.	p				•														Ct.
Rubus procerus P. J. Muell.	p															•			Md.
Amorpha herbacea Walt.	p	•			•	•	•	•						•		•			N. C.
Astragalus michauxii Kuntze	p													•	•				N. C.
Baptisia alba (L.) R. Br.	p		•	•	•														Va.
Baptisia cinerea (Raf.) Fern. & Schub.	p		•		•		•	•	•	•	•	•	•	•	•	•			Va.
Baptisia perfoliata (L.) R. Br.	p	•	•	•															S. C.
Baptisia tinctoria (L.) R. Br.	p		•	•	•	•	•	•	•		•	•		•	•	•	•	•	Can.
Cassia nictitans L.	a				•	•		•	•	•	•	•		•		•	•	•	Vt.
Cassia fasciculata Michx.	a	•	•	•		•					•	•				•	•		Can.
Cassia tora L.	a		•					•											Pa.
Centrosema virginianum (L.) Benth.	p	•	•		•			•	•		•								N. J.
Clitoria mariana L.	p						•			•		•	•	•	•	•		•	N. Y.
Crotalaria angulata Mill.	p		•	•	•	•		•		•						•			Va.
Crotalaria intermedia Kotschy	a			•															N. C.
Crotalaria purshii DC.	p			•		•	•												Va.
Crotalaria spectabilis Roth	a				•						•			•					Va.
Crotalaria sagittalis L.	p																•		Va.
Desmodium canescens (L.) DC.	p	•						•								•		•	Can.
Desmodium tortuosum (Sw.) DC.	a				•														N. C.
Desmodium strictum (Pursh) DC.	p	•			•	•		•	•	•	•	•	•	•		•		•	N. J.
Desmodium ciliare (Muhl.) DC.	p				•									•		•			N. E.
Desmodium lineatum DC.	p				•														Md.
Galactia erecta (Walt.) Vail	p	•		•											•				N. C.
Galactia mollis Michx.	p	•	•																N. C.
Galactia regularis (L.) BSP.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	N. Y.
Galactia volubilis (L.) Britt.	p		•	•		•											•	•	N. Y.
Indigofera caroliniana Mill.	p	•	•	•		•	•	•	•		•					•			N. C.
Lupinus diffusus Nutt.	p	•	•	•	•	•	•	•		•	•	•	•	•	•				N. C.
Lupinus perennis L.	p																•	•	Can.
Lespedeza capitata Michx.	p													•	•				Can.
Lespedeza cuneata (Dumont) G. Don	p		•		•	•		•			•				•				Pa.
Lespedeza hirta (L.) Hornem.	p	•	•	•	•		•			•	•	•	•	•	•	•		•	Can.
Lespedeza procumbens Michx.	p		•		•		•		•	•		•	•						N. H.

Table I—Continued

SPECIES	DURATION	Richmond Co., Ga.	Aiken Co., S. C.	Lexington Co., S. C.	Richland Co., S. C.	Kershaw Co., S. C.	Darlington Co., S. C.	Chesterfield Co., S. C.	Marlboro Co., S. C.	Scotland Co., N. C.	Richmond Co., N. C.	Moore Co., N. C.	Hoke Co., N. C.	Cumberland Co., N. C.	Harnett Co., N. C.	Wayne Co., N. C.	Gates Co., N. C.	Nansemond Co., N. C.	NORTHEASTERN LIMIT
Lespedeza repens (L.) Bart.	p	•	•	•	•	•		•		•		•	•	•	•	•	•	•	Ct.
Lespedeza stipulacea Maxim.	a	•							•	•			•	•					Pa.
Lespedeza striata (Thunb.) H. & A.	a	•						•		•	•				•				N. J.
Lespedeza stuevei Nutt.	p	•	•							•				•					Mass.
Lespedeza virginica (L.) Britt.	p	•	•				•	•						•	•	•		•	N. H.
Petalostemon pinnatum (Walt.) Blake	p	•		•				•	•	•	•	•	•	•	•	•			N. C.
Phaseolus sinuatus Nutt.	p									•									N. C.
Psoralea canescens Michx.	p			•															N. C.
Psoralea lupinellus Michx.	p									•	•	•	•						N. C.
Psoralea psoralioides (Walt.) Cory	p					•					•					•			Va.
Rhynchosia simplicifolia (Walt.) Wood	p	•	•	•			•	•	•	•	•				•	•			N. C.
Rhynchosia tomentosa (L.) H. & A.	p		•																Del.
Rhynchosia difformis (Ell.) DC.	p																	•	Va.
Robinia nana (Ell.) Spach.	p	•	•	•	•							•		•					N. C.
Schrankia microphylla (Dryander) MacBr.	p	•	•	•		•	•	•	•	•	•					•			Va.
Glottidium vesicarium (Jacq.) Harper	a			•															N. C.
Stylosanthes biflora (L.) BSP.	p	•	•		•	•	•	•	•	•	•	•	•		•	•			N. Y.
Stylosanthes riparia Kearney	p			•			•	•							•				N. J.
Trifolium arvense L.	a		•																Can.
Tephrosia florida (F. G. Dietr.) C. E. Wood.	p		•	•	•	•	•	•	•	•	•	•				•			N. C.
Tephrosia spicata (Walt.) T. & G.	p	•	•			•	•				•			•	•	•		•	Del.
Tephrosia virginiana (L.) Pers.	p	•	•	•	•	•	•	•	•	•	•	•	•	•		•	•	•	Can.
Zornia bracteata (Walt.) Gmel.	p	•	•	•		•				•									Va.
Linum medium (Planch.) Britt.	p						•												Can.
Linum virginianum L.	p														•				Can.
Oxalis dillenii (L.) Eiton	a	•																	Can.
Geranium carolinianum L.	a		•	•															Mass.
Melia azederach L.	p				•														Va.
Polygala grandiflora Walt.	p	•	•			•					•								N. C.
Polygala incarnata L.	a					•													Can.
Polygala lutea L.	b														•	•			N. Y.
Polygala nana (Michx.) DC.	v			•															S. C.
Polygala polygama Walt.	v			•	•														N. J.
Polygala mariana Mill.	a					•													N. J.
Polygala nuttallii T. & G.	a													•					N. E.
Cnidoscolus stimulosus (Michx.) Gray	p	•		•	•		•	•	•	•	•	•	•	•	•	•	•	•	Va.
Croton capitatus Michx.	a				•														N. Y.
Croton glandulosus L.	a	•	•	•		•	•					•		•		•			N. J.
Acalypha gracilens Gray	a		•	•															N. H.
Tragia urens L.	p	•	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	Va.
Tragia urticifolia Michx.	p	•	•		•			•											Va.
Stillingia sylvatica L.	p	•	•	•	•	•	•		•	•	•	•	•	•	•	•		•	Va.
Euphorbia corollata L.	p	•	•	•	•			•			•	•		•		•			Can.
Euphorbia curtisii Engelm.	p		•	•	•	•	•	•	•	•	•	•	•		•				N. C.
Euphorbia eriogonoides (Small) Small.	p											•					•		N. C.
Euphorbia gracilior Ell.	p	•	•	•		•		•							•				N. C.
Euphorbia ipecacuanhae L.	p	•		•	•			•		•	•	•	•	•		•	•	•	N. Y.
Chamaesyce maculata (L.) Small.	a	•	•																Can.
Chamaesyce supina (Raf.) Moldenke.	a		•																Can.

Table I—Continued

SPECIES	DURATION	Richmond Co., Ga.	Aiken Co., S. C.	Lexington Co., S. C.	Richland Co., S. C.	Kershaw Co., S. C.	Darlington Co., S. C.	Chesterfield Co., S. C.	Marlboro Co., S. C.	Scotland Co., N. C.	Richmond Co., N. C.	Moore Co., N. C.	Hoke Co., N. C.	Cumberland Co., N. C.	Harnett Co., N. C.	Wayne Co., N. C.	Gates Co., N. C.	Nansemond Co., N. C.	NORTHEASTERN LIMIT
Ceratiola ericoides Michx.	p		•	•	•	•									•				S. C.
Rhus aromatica Ait.	p	•																	Can.
Rhus copallina L.	p	•	•	•	•	•	•	•	•		•	•		•		•	•		N. Y.
Rhus radicans L.	p					•													Can.
Rhus toxicodendron L.	p	•	•		•	•		•		•	•	•	•	•	•	•	•	•	N. J.
Cyrilla racemiflora L.	p		•	•											•				Va.
Ilex glabra (L.) Gray	p				•	•	•					•			•		•		N. S.
Ilex opaca Ait.	p																•	•	Mass.
Ilex vomitoria Ait.	p		•					•											Va.
Ceanothus americanus L.	p	•							•			•			•	•			Can.
Vitis rotundifolia Michx.	p	•	•	•			•	•		•		•		•			•	•	Del.
Vitis aestivalis Michx.	p																•		Mass.
Sida rhombifolia L.	a	•	•			•													Va.
Hypericum denticulatum Walt.	p		•	•															N. J.
Hypericum galioides Lam.	p		•	•												•			N. C.?
Hypericum gentianoides (L.) BSP.	a	•	•	•	•	•	•	•	•	•	•	•		•	•	•			Can.
Hypericum punctatum Lam.	p	•																	Can.
Hypericum setosum L.	p																•		Va.
Ascyrum hypericoides L.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	Mass.
Ascyrum stans Michx.	p															•			N. Y.
Helianthemum canadense (L.) Michx.	p	•				•			•	•				•	•	•	•	•	N. S.
Helianthemum rosmarinifolium Pursh	p	•	•	•	•	•		•											S. C.
Lechea villosa Ell.	b	•	•	•	•	•		•	•	•				•	•	•			Can.
Lechea patula Leggett?	b	•				•	•	•	•	•	•	•	•	•					N. C.?
Lechea racemulosa Michx.	b		•	•										•					N. Y.
Lechea tenuifolia Michx.	b		•		•														Me.
Viola pedata L.	p		•	•				•							•				Can.
Viola septemloba LeConte	p	•		•															Va.
Passiflora incarnata L.	p	•	•		•		•				•						•		Pa.
Opuntia humifusa Raf.	p	•	•	•	•	•	•	•				•		•		•	•	•	Mass.
Nyssa sylvatica Marsh.	p		•															•	N. E.
Rhexia alifanus Walt.	p						•					•							N. C.
Rhexia mariana Walt.	p					•						•							Mass.
Gaura filipes Spach	p	•	•	•	•	•													S. C.
Oenothera laciniata Hill	a	•	•	•											•				N. E.
Oenothera fruticosa L.	p									•									Ct.
Oenothera arenicola Coker	p							•						•	•				N. C.
Aralia spinosa L.	p																•		N. E.
Eryngium yuccifolium Michx.	p		•																Ct.
Eryngium synchaetum (Gray) Rose	p	•																	S. C.
Spermolepis divaricata (Walt.) Raf.	a		•	•	•			•											N. C.
Angelica venenosa (Greenway) Fern.	p		•	•								•			•				Ct.
Daucus carota L.	b	•																	Can.
Cornus florida L.	p						•			•									Me.
Clethra alnifolia L.	p			•	•		•	•		•		•			•	•		•	Me.
Rhododendron atlanticum (Ashe) Rehd.	p																•		N. J.
Rhododendron viscosum (L.) Torr.	p															•		•	Va.?
Leiophyllum buxifolium (Berg.) Ell.	p			•															N. J.

Table I—Continued

SPECIES	DURATION	Richmond Co., Ga.	Aiken Co., S. C.	Lexington Co., S. C.	Richland Co., S. C.	Kershaw Co., S. C.	Darlington Co., S. C.	Chesterfield Co., S. C.	Marlboro Co., S. C.	Scotland Co., N. C.	Richmond Co., N. C.	Moore Co., N. C.	Hoke Co., N. C.	Cumberland Co., N. C.	Harnett Co., N. C.	Wayne Co., N. C.	Gates Co., N. C.	Nansemond Co., N. C.	NORTHEASTERN LIMIT
Kalmia angustifolia L.	p															•	•	•	Nfld.
Kalmia latifolia L.	p		•					•		•									N. E.
Lyonia mariana (L.) D. Don.	p			•	•		•	•	•			•		•	•	•	•		Ct.
Epigaea repens L.	p		•							•				•	•				N. E.
Gaultheria procumbens L.	p																•		Nfld.
Gaylussacia baccata (Wang.) K. Koch	p																•		Nfld.
Gaylussacia dumosa (Andr.) T. & G.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		Nfld.
Gaylussacia frondosa (L.) T. & G.	p																•		N. H.
Vaccinium arboreum Marsh.	p	•	•	•	•	•	•	•						•		•			Va.
Vaccinium corymbosum L.	p										•						•		N. S.
Vaccinium crassifolium Andr.	p						•									•			Va.
Vaccinium stamineum L.	p	•	•	•	•									•		•	•	•	Can.
Vaccinium tenellum Ait.	p						•	•							•	•	•	•	Va.
Vaccinium vacillans Torr.	p																•	•	N. S.
Pyxidanthera barbulata Michx.	p														•	•			N. J.
Diospyros virginiana L.	p	•	•	•	•	•	•	•			•	•		•			•	•	N. E.
Symplocos tinctoria (L.) L'Her.	p																•		Del.
Polypremum procumbens L.	p	•	•	•	•			•	•			•		•		•			N. Y.
Gelsemium sempervirens (L.) Ait.	p						•										•	•	Va.
Sabatia brachiata Ell.	v		•	•		•	•	•			•	•	•	•	•				Va.
Sabatia quadrangula Wilbur	v		•	•	•		•	•		•			•						N. J.
Amsonia ciliata Walt.	p	•	•	•	•		•	•			•								N. C.
Apocynum cannabinum L.	p				•							•							Can.
Asclepias amplexicaulis Sm.	p	•	•	•	•	•	•	•		•	•	•		•	•	•		•	N. H.
Asclepias humistrata Walt.	p	•			•					•	•					•			N. C.
Asclepias tuberosa L.	p	•	•	•	•		•	•								•	•	•	Can.
Asclepias verticillata L.	p	•			•														Can.
Breweria humistrata (Walt.) Gray	p	•	•	•	•	•	•	•	•	•	•	•		•	•				Va.
Breweria michauxii Fern. & Schub.	p	•			•				•			•							Va.?
Breweria pickeringii (Torr.) Gray	p	•								•	•								N. J.
Ipomea pandurata (L.) G. F. W. Meyer	p							•			•	•	•			•			Can.
Ipomea lacunosa L.	a													•					Pa.
Phlox drummondii Hook.	a		•																N. C.
Phlox nivalis Lodd.	p	•		•	•	•				•		•						•	Va.
Heliotropium amplexicaule Vahl	p	•	•																N. C.
Onosmodium virginianum (L.) A. DC.	p			•		•				•									Mass.
Lithospermum caroliniense (Walt.) MacM.	p	•	•	•															Va.
Verbena bonariensis L.	p		•																N. C.
Verbena carnea Medic.	p	•	•	•						•									Va.
Verbena tenuisecta Briq.	p	•																	N. C.
Callicarpa americana L.	p		•																Md.
Salvia azurea Lam.	p	•	•	•	•	•	•												N. C.
Salvia lyrata L.	p	•																	Ct.
Trichostema dichotomum L.	a						•								•	•	•	•	Me.
Trichostema setaceum Houtt.	a	•		•		•													Ct.
Scutellaria incana Biehler?	p			•															N. Y.
Pycnanthemum setosum Nutt.	p								•			•							N. J.
Physalis lanceolata Michx.	p	•	•	•	•	•		•		•			•	•		•			N. C.

Table I—Continued

SPECIES	DURATION	Richmond Co., Ga.	Aiken Co., S. C.	Lexington Co., S. C.	Richland Co., S. C.	Kershaw Co., S. C.	Darlington Co., S. C.	Chesterfield Co., S. C.	Marlboro Co., S. C.	Scotland Co., N. C.	Richmond Co., N. C.	Moore Co., N. C.	Hoke Co., N. C.	Cumberland Co., N. C.	Harnett Co., N. C.	Wayne Co., N. C.	Gates Co., N. C.	Nansemond Co., N. C.	NORTHEASTERN LIMIT
Solanum carolinense L.	p																	•	Can.
Linaria canadensis (L.) Dumont	v		•	•				•		•		•				•	•	•	Can.
Penstemon australis Small	p	•		•	•				•			•		•					Va.
Seymeria cassioides (Walt.) Blake	a													•		•			Va.
Seymeria pectinata Pursh	a			•															N. C.
Gerardia fasciculata Ell.	a	•	•		•	•													S. C.
Gerardia pectinata (Nutt.) Benth.	b	•	•	•	•	•	•	•	•	•	•		•	•	•			•	Va.
Gerardia pedicularia L.	b									•	•	•	•	•	•	•	•		Me.
Gerardia pinetorum (Pennell) Britt. & Wils.	a	•																	Ga.
Gerardia purpurea L.	a																	•	N. E.
Gerardia setacea (Walt.) J. F. W. Gmel.	a		•			•	•	•	•	•	•	•	•		•	•	•	•	N. Y.
Campsis radicans (L.) Seem.	p		•																Ct.
Dyschoriste oblongifolia (Michx.) Ktze.	p	•	•																S. C.
Ruellia caroliniensis (Walt.) Steud.	a					•													N. J.
Plantago aristata Michx.	a				•				•	•	•	•	•	•	•				N. E.
Plantago hookeriana var. nuda (Gray) Poe	a	•	•	•					•		•			•					N. C.
Plantago lanceolata L.	p												•						Can.
Plantago virginica L.	a							•											Me.
Galium pilosum Ait.	p	•	•	•		•			•			•			•			•	Can.
Richardia scabra L.	p	•		•				•	•		•			•		•			Va.
Diodia teres Walt.	a	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		•	R. I.
Houstonia longifolia Gaertn.	p	•	•	•	•	•			•		•		•	•					Me.
Valerianella radiata (L.) Dufr.	a			•															Mass.
Wahlenbergia marginata (Thunb.) A. DC.	p		•			•			•										N. C.
Specularia perfoliata (L.) A. DC.	a	•	•	•				•			•							•	Me.
Lobelia nuttallii R. & S.	p				•		•			•				•				•	N. Y.
Vernonia angustifolia Michx.	p	•	•	•	•	•	•	•	•	•	•	•	•						N. C.
Vernonia acaulis (Walt.) Gleason	p			•	•	•	•	•	•	•		•		•					N. C.
Vernonia acaulis x angustifolia	p					•								•					N. C.
Elephantopus carolinianus Willd.	p														•	•			N. J.
Elephantopus tomentosus L.	p			•															Md.
Eupatorium album L.	p	•	•	•	•		•	•	•	•	•	•	•	•	•			•	N. J.
Eupatorium aromaticum L.	p	•	•		•		•			•		•		•					Mass.
Eupatorium capillifolium (Lam.) Small	a													•				•	Mass.
Eupatorium compositifolium Walt.	p	•			•		•			•	•	•							N. C.
Eupatorium hyssopifolium L.	p	•		•	•		•		•			•		•		•			Mass.
Eupatorium linearifolium Walt.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•				Va.
Eupatorium pilosum Walt.	p														•	•			N. E.
Eupatorium rotundifolium L.	p				•	•	•	•	•	•		•	•		•				N. J.
Eupatorium semiserratum DC.	p			•															Va.
Liatris aspera Michx.	p		•																Can.
Liatris earlei (Greene) K. Schum.	p			•															Va.?
Liatris graminifolia (Walt.) Willd.	p		•	•		•		•	•	•	•	•	•	•	•	•			N. J.
Liatris microcephala (Small) K. Schum.	p												•						N. C.
Liatris regiomontis (Small) K. Schum.	p				•	•									•				N. C.
Liatris secunda Ell.	p	•	•	•	•	•	•	•	•		•								N. C.
Liatris spicata (L.) Willd.	p			•	•													•	N. E.
Liatris squarrosa (L.) Michx.	p	•	•		•							•		•					Del.

Table I—Continued

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Liatris tenuifolia Nutt.	p	•	•	•	•	•	•		•										S. C.
Carphephorus bellidifolius (Michx.) Torr. & Gray	p	•		•	•	•	•	•	•	•	•		•	•	•	•	•	•	Va.
Carphephorus tomentosus (Michx.) Torr. & Gray	p															•			Va.
Trilisa odoratissima (Walt.) Cass	p															•			Va
Heterotheca subazillaris (Lam.) Britt. & Rusby	v	•	•	•	•	•			•										N. J.
Chrysopsis gossypina Nutt.	p	•	•	•	•	•	•			•	•		•	•	•	•			N. C.
Chrysopsis gossypina f. decumbens (Chapm.) Godfrey	p								•			•				•			N. C.
Chrysopsis graminifolia (Michx.) Ell.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			Va.
Chrysopsis mariana (L.) Ell.	p	•				•	•			•						•	•	•	N. Y.
Chrysopsis nervosa (Willd.) Ell.	p								•	•	•			•			•	•	Del.
Chrysopsis pinifolia Ell.	p										•	•			•	•			N. C.
Solidago bootii Hook.	p		•			•								•		•		•	Va.
Solidago microcephala (Greene) Bush	p				•		•	•	•			•		•		•		•	N. J.
Solidago nemoralis Ait.	p				•	•													Can.
Solidago odora Ait.	p	•	•	•	•	•	•	•	•	•				•		•	•		N. H.
Haplopappus divaricatus (Nutt.) Gray	a	•	•	•	•	•		•	•		•	•	•	•	•	•		•	Va.
Aster concolor L.	p	•	•			•	•	•	•	•		•		•	•				Mass.
Aster dumosus L.	p				•		•			•						•			Me.
Aster lateriflorus (L.) Britt.	p											•							N. S.
Aster linariifolius L.	p	•	•	•	•	•	•	•	•	•	•	•	•			•	•	•	Can.
Aster patens Ait.	p						•												Me.
Aster squarrosus Walt.	p													•	•				N. C.
Aster undulatus L.	p																	•	N. S.
Erigeron canadensis L.	a										•								Can.
Erigeron linifolius Willd.	a		•																N. C.?
Erigeron pusillus Nutt.	a	•		•	•	•	•	•		•	•		•			•	•	•	Mass.
Erigeron strigosus Muhl.	p	•	•	•	•		•	•	•		•	•	•	•	•	•			Can.
Sericocarpus asteroides (L.) BSP.	p		•	•	•		•	•	•	•	•	•		•	•	•		•	Me.
Sericocarpus bifoliatus (Walt.) Porter	p	•	•	•		•	•	•	•	•	•	•		•	•	•			N. C.
Sericocarpus linifolius (L.) BSP.	p		•	•			•								•	•			N. H.
Coreopsis lanceolata L.	p			•								•							Va.
Coreopsis major Walt.	p	•	•	•	•	•	•	•	•	•	•	•	•						Va.
Coreopsis verticillata L.	p											•	•	•	•				Md.
Marshallia obovata (Walt.) Beadle & Boyn.	p		•	•	•					•									N. C.
Baccharis halimifolia L.	p				•														Mass.
Gnaphalium falcatum Lam.?	a					•													S. C.
Gnaphalium obtusifolium L.	b	•	•	•	•	•	•	•	•		•			•	•				N. S.
Gnaphalium purpureum L.	a	•	•	•	•				•	•			•		•	•		•	N. E.
Antennaria fallax Greene	p											•							Me.
Acanthospermum australe (Loefl.) Ktze.	a	•	•	•	•			•			•								Mass.
Ambrosia artemesiifolia L.	a			•				•			•	•		•	•		•		Nfld.
Ambrosia coronopifolia T. & G.	p	•																	N. S.
Silphium asteriscus L.	p	•																	Va.
Silphium compositum Michx.	p	•	•		•	•	•	•		•	•	•	•	•	•	•			Va.

Table I—Continued

SPECIES	DURATION	Richmond Co., Ga.	Aiken Co., S. C.	Lexington Co., S. C.	Richland Co., S. C.	Kershaw Co., S. C.	Darlington Co., S. C.	Chesterfield Co., S. C.	Marlboro Co., S. C.	Scotland Co., N. C.	Richmond Co., N. C.	Moore Co., N. C.	Hoke Co., N. C.	Cumberland Co., N. C.	Harnett Co., N. C.	Wayne Co., N. C.	Gates Co., N. C.	Nansemond Co., N. C.	NORTHEASTERN LIMIT
Silphium dentatum Ell.	p	•																	S. C.
Berlandiera pumila (Michx.) Nutt.	p		•	•	•	•	•	•											S. C.
Tetragonotheca helianthoides L.	p	•		•															Va.
Parthenium integrifolium L.	p					•		•											Mass.
Rudbeckia divergens T. V. Moore	p	•																	S. C.
Rudbeckia hirta L.	p		•																Mass.
Helianthus atrorubens L.	p								•			•		•	•				Va.
Helianthus divaricatus L.	p	•	•	•							•			•					Me.
Helianthus debilis Nutt.	a				•														Me.
Hymenopappus scabiosaeus L'Her.	v	•	•																S. C.
Helenium amarum (Raf.) Rock.	a	•	•		•			•	•				•	•		•			Mass.
Gaillardia lanceolata Michx.	a	•	•																S. C.
Senecio smallii Britt.	p	•		•			•	•		•	•								N. J.
Cirsium repandum Michx.	b	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			Va.
Krigia virginica (L.) Willd.	a	•	•					•	•	•		•		•		•			Me.
Lactuca graminifolia Michx.	a	•	•	•	•	•				•	•		•		•				N. J.
Lactuca canadensis L.	b				•			•							•				N. S.
Lactuca scariola L.	a												•						Can.
Hieracium gronovii L.	p		•		•	•		•								•			Mass.
Hieracium venosum L.	p						•	•	•	•	•	•		•	•	•			Me.
Hieracium venosum x gronovii	p		•				•	•	•		•							•	Mass.
Pyrrhopappus carolinianus (Walt.) DC.	v	•		•	•														Del.
Arundinaria tecta (Walt.) Muhl.	p							•							•				N. J.
Festuca myuros L.	a			•															Mass.
Festuca octoflora Walt.	a	•	•	•	•			•										•	Can.
Eragrostis curvula (Schrad.) Nees?	p			•															N. C.
Eragrostis hirsuta (Michx.) Nees.	p	•		•		•		•								•	•		Va.
Eragrostis orcuttiana Vasey?	a			•															S. C.?
Eragrostis refracta (Muhl.) Scribn.	p	•	•	•					•							•			Del.
Eragrostis spectabilis (Pursh) Steud.	p	•		•	•			•	•		•	•	•		•				Mass.
Triplasis americana Beauv.	p	•	•	•	•	•	•			•	•					•			N. C.
Triplasis purpurea (Walt.) Chapm.	a	•								•						•		•	Me.
Hordeum pusillum Nutt.	a				•														Del.
Danthonia sericea Nutt.	p			•	•												•		N. J.
Danthonia spicata (L.) Beauv.	p																•		Nfld.
Avena sativa L.	a	•																	Can.
Stipa avenacea L.	p		•														•	•	Mass.
Sporobolus clandestinus (Biehler) Hitchc.	p																•		Ct.
Sporobolus junceus (Michx.) Kunth.	p	•	•	•	•	•	•	•	•	•	•		•						N. C.
Sporobolus poiretii (R. & S.) Hitchc.	p					•													Va.
Sporobolus teretifolius Harper?	p					•													S. C.
Muhlenbergia expansa (DC.) Trin.	p									•									Va.
Agrostis perennans (Walt.) Tuckerh.	p				•														Can.
Agrostis hiemalis (Walt.) BSP.	p									•									Mass.
Aristida dichotoma Michx.	a				•								•		•	•			N. E.
Aristida lanosa Muhl.	p		•																N. J.
Aristida affinis (Schultes) Kunth.	p				•														N. C.
Aristida purpurascens Poir.	p	•	•	•	•	•			•		•	•	•	•		•	•	•	Mass.

Table I—Continued

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Aristida stricta Michx.	p						•	•	•	•	•	•	•	•	•	•			N. C.
Aristida longespica Poir.	a				•				•				•						N. H.
Aristida tuberculosa Nutt.	a	•	•	•	•	•					•								Mass.
Cynodon dactylon (L.) Pers.	p											•	•			•		•	Can.
Eleusine indica (L.) Gaertn.	a													•					Can.
Gymnopogon ambiguus (Michx.) BSP.	p	•	•	•	•		•		•	•		•	•		•	•			N. J.
Anthaenantia villosa (Michx.) Beauv.	p	•				•		•					•						N. C.
Digitaria filiformis (L.) Koel.	a	•								•			•		•		•		N. H.
Digitaria ischaemum (Schreb.) Muhl.	a				•												•		Md.
Digitaria sanguinalis (L.) Scop.	a	•		•	•	•		•		•	•	•		•	•			•	Can.
Digitaria villosa (Walt.) Pers.	p								•										Md.
Leptoloma cognatum (Schultes) Chase	p	•		•	•	•			•	•	•	•	•			•			N. H.
Paspalum boscianum Flugge	a													•					Va.
Paspalum ciliatifolium Michx.	p	•		•		•			•										N. H.
Paspalum dilatatum Poir.	p			•				•											Va.
Paspalum floridanum Michx.	p	•	•	•				•											Va.
Paspalum pubescens Muhl.	p	•		•				•											Vt.
Paspalum setaceum Michx.	p		•															•	Mass.
Paspalum urvillei Steud.	p		•																Va.
Panicum aciculare Desv.	p													•	•				N. J.
Panicum addisoni Nash.	p	•		•		•			•		•				•	•	•	•	Va.
Panicum albomarginatum Nash.	p							•											Va.
Panicum ashei Pears.	p		•	•	•														Mass.
Panicum ciliatum Ell.	p														•				N. C.
Panicum commonsianum Ashe.	p					•									•	•			Mass.
Panicum columbianum Scribn.	p				•														Mass.
Panicum linearifolium Scribn.	p													•					Can.
Panicum malacon Nash.	p	•	•								•								N. C.
Panicum portoricense Desv.	p							•										•	Va.?
Panicum pseudopubescens Nash.	p					•													Conn.
Panicum oligosanthes Schultes.	p		•	•															Mass.
Panicum ravenelii Scribn. & Merr.	p						•												Del.
Panicum scoparium Lam.	p							•	•										Mass.
Panicum sphaerocarpon Ell.	p				•					•				•					Vt.
Panicum tenue Muhl.	p	•								•									N. C.
Panicum trifolium Nash.	p												•						N. J.
Panicum tsugetorum Nash.	p		•	•															Me.
Panicum verrucosum Muhl.	a																•		Mass.
Panicum zalapense HBK.	p																•		Md.
Sacciolepis striata (L.) Nash.	p							•											N. J.
Setaria geniculata (Lam.) Beauv.	p	•																	Mass.
Setaria lutescens (Weigel) Hubb.	a	•																	Can.
Cenchrus echinatus L.	a					•													N. C.
Cenchrus incertus Curtis.	p		•					•											Va.
Cenchrus pauciflorus Benth.	a	•	•	•				•			•								Can.
Andropogon gerardi Vitman.	p	•																	Can.
Andropogon scoparius Michx.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	N. H.
Andropogon ternarius Michx.	p		•		•	•	•			•	•	•		•	•	•	•	•	N. J.
Andropogon virginicus L.	p	•		•	•														Mass.

Table I—Continued

SPECIES	DURATION	Richmond Co., Ga.	Aiken Co., S. C.	Lexington Co., S. C.	Richland Co., S. C.	Kershaw Co., S. C.	Darlington Co., S. C.	Chesterfield Co., S. C.	Marlboro Co., S. C.	Scotland Co., N. C.	Richmond Co., N. C.	Moore Co., N. C.	Hoke Co., N. C.	Cumberland Co., N. C.	Harnett Co., N. C.	Wayne Co., N. C.	Gates Co., N. C.	Nansemond Co., N. C.	NORTHEASTERN LIMIT
Andropogon elliottii Chapm.	p						•	•	•	•		•	•				•	•	N. J.
Sorghum halopense (L.) Pers.	p		•																N. E.
Sorghastrum elliottii (Mohr) Nash	p	•																	Md.
Bulbostylis barbata (Rottb.) Clarke	a			•	•	•		•											N. C.?
Bulbostylis capillaris (L.) Clarke	a	•				•		•											Can.
Bulbostylis ciliatifolia (Ell.) Fern.	a	•	•	•	•	•		•	•	•		•	•	•	•	•	•	•	Va.
Bulbostylis stenophylla (Ell.) Clarke	a																•		N. C.
Cyperus compressus L.	a					•													N. Y.
Cyperus dipsaciformis Fern.	p	•	•	•				•	•	•	•		•						N. J.
Cyperus filiculmis Vahle	p	•	•	•	•	•	•					•				•	•	•	Can.
Cyperus grayii Torr.	p																	•	Mass.
Cyperus iria L.	a															•			Va.
Cyperus ovularis (Michx.) Torr.	p	•																	N. Y.
Cyperus retrofractus (L.) Torr.	p				•														N. J.
Cyperus retrorsus Chapm.	p	•			•										•		•	•	N. J.
Cyperus rotundus L.	p							•											N. Y.
Carex albolutescens Schw.	p																•		N. S.
Carex complanata Torr. & Hook.	p																•		N. J.
Carex nigromarginata Schw.	p																•		Ct.
Carex tenax Chapm.	p	•	•	•															S. C.
Carex virescens Muhl.?	p																•		Can.
Rhynchospora grayi Kunth	p	•	•	•	•	•	•	•		•	•	•	•	•	•	•			Va.
Schleria ciliata Michx.	p						•												Va.
Scleria nitida Willd.	p		•					•							•				N. J.
Scleria pauciflora Muhl.	p			•															N. H.
Xyris torta Small	p															•	•		N. H.
Lachnocaulon anceps (Walt.) Morong	p																•		Va.
Commelina erecta L.	p	•	•			•													N. Y.
Tradescantia ohioensis Raf.	p		•																Mass.
Tradescantia rosea var. *graminea* (Small) A. & W.	p	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			Va.
Juncus acuminatus Michx.	p															•		•	Me.
Juncus biflorus Ell.	p															•			Mass.
Juncus canadensis J. Gay	p										•								N. S.
Juncus secundus Beauv.	p			•	•				•	•		•				•		•	Me.
Aletris farinosa L.	p						•							•	•				N. H.
Allium cuthbertii Small	p	•	•																N. C.
Amianthium muscaetoxicum (Walt.) Ktze.	p	•																	N. Y.
Nolina georgiana Michx.	p	•																	S. C.
Smilax bona-nox L.	p	•																	Md.
Smilax glauca Walt.	p	•	•	•	•							•		•			•	•	N. J.
Smilax rotundifolia L.	p																•		Me.
Yucca smalliana Fern.?	p	•	•		•														N. C.
Iris verna L.	p		•		•			•	•	•	•	•	•	•	•	•			Md.
Sisyrinchium fibrosum Bickn.	p			•											•		•	•	Va.
Sisyrinchium rufipes Bickn.	p						•	•	•	•	•	•	•		•				N. C.
Hypoxis hirsuta (L.) Coville	p										•								Va.
Hypoxis rigida Chapm.	p											•							N. C.
Spiranthes tuberosa Raf.	p		•	•															N. J.

areas of the Citronelle formation makes this theory of derivation somewhat doubtful. Limestone is rarely associated with fluvial fans, and the Citronelle of the Carolina fall-line hills is believed to represent coalesced alluvial fans (Doering, 1958). It must be noted, however, that some of the Eocene formations underlying the Citronelle formation do contain limestone. Analyses of components of the Norfolk and Orangeburg soils presented in the *Atlas of American Agriculture* show that the Orangeburg is richer in clay minerals and poorer in silica than the Norfolk soil. The more argillaceous Orangeburg soil often supports plant communities similar to some of those of the piedmont, plus some admixture of the more mesophytic sandhill elements. Such is also true of the Eocene red hills of Georgia (Thorne, 1949).

Wells and Shunk (1931), in their most valuable study of the Carolina sandhills, have pointed out that the flora of the sandhills is probably determined by the inability of alien roots to grow rapidly enough through the sterile surface soils to reach richer, moister layers below:

> Under a low nutrient condition which inhibits growth, only those plants can survive which restrict water outgo, since in the sand, the roots with inhibited growth may reach only a limited amount of water. . . . In connection with the sterility problem, attention may well be again directed to the concomitant factors of low bacterial count, low CO_2 evolution, low total N, and extremely high C/N ratio.

These factors are apparently most effective in the seedling stages, and a short drought would eliminate seedlings of mesophytic species quite effectively; prolonged droughts might even eliminate the seedlings of the xerophytic species.

Phenology

The fall-line sandhills are truly barren in the spring, with little flowering except some of the arboreal and ruderal species, but "barren" is hardly an appropriate adjective later in the season, for, as Coker (1912) noted, with the exception of the savannas, the sandhills are the "most colorful of all the floristic regions of our section." Flowering, hardly under way until June, seems to increase gradually; the third largest sandhill family, the legumes, culminates its flowering in July and August, and the largest and second largest families, the composites and the grasses, flower most prominently in September. The relative paucity of the spring flora is probably to be correlated with the open nature of the habitat.

Harper (1906), writing of the Altamaha Grit region of Georgia, said, "On the sand-hills ... the annual plants mostly bloom between July 1st and October 1st. ... The height of the flowering seems to be in September. The average length of the flowering period (of a species) is 51 days." Harshberger (1916), who laboriously graphed the phenological phenomena of 548 pine barren plants of New Jersey, published data indicating that, even as far north as New Jersey, the culmination of flowering occurs in August. It seems safe to conclude that, in the xeric sands of the Carolina sandhills, the culmination of flowering is in September.

Analysis of Table I reveals that over 75 per cent of the sandhill species are perennials. The sandhills share this high proportion of perenniality with the outer dunes of the Atlantic Coast. It is tempting to speculate whether this high degree of perenniality is directly or, more probably, indirectly related to the high C/N ratio of the sandhills, a ratio which causes an increase in woodiness and in the root/shoot ratio. This temptation to conjecture is enhanced when one considers that several species are perennial at one end of their ranges and annual at the other end.

Most of the sandhill annuals occur in ruderal situations. In the high degree of perenniality, the sandhills contrast vividly with the western deserts, which have a rather high percentage of ephemeral annuals, perhaps because of the scarcity and irregularity of precipitation.

Morphology

Several presumably adaptive characters, perhaps reflecting the selective effects of xerism, have been suggested for the sandhill flora. Many (Harper, 1906; Penfound and Watkins, 1937; Braun, 1950) have noticed the high number of evergreens in the coastal plain flora which are responsible for the title "Southeastern Evergreen Forest." The sandhills, however, have fewer evergreens than some other coastal plain habitats, such as shrub bogs and maritime forests; furthermore, the evergreen condition is not necessarily adaptive.

The involute leaves of grasses, such as the herbaceous dominants, the wiregrasses, *Aristida* spp. and *Sporobolus junceus* (Michx.) Kunth, are

often functional in water conservation. The sandhills also contain a high percentage of tortifoliates, *e.g.*, *Quercus laevis* Walt., *Baptisia perfoliata* (L.) R. Br., *B. cinera* (Raf.) Fern. & Schub., *Asclepias humistrata* Walt., *Gelsemium sempervirens* (L.) Ait., *Physalis lanceolata* Michx., *Eupatorium linearifolium* Walt., *Solidago odora* Ait., *Solidago tortifolia* Ell. and *Sericocarpus bifoliatus* (Walt.) Porter. In the tortifoliates, by a twisting of the leaves or the stems, the leaves are so disposed that they receive only a fraction of the incident light rays. Wells and Shunk (1931) demonstrated, by tying the leaves of *Quercus laevis* in a horizontal plane, that more direct insolation was actually deleterious to the leaves. *Eupatorium album* L., *E. leucolepis* Torr. & Gray, *Verbena carnea* Medic., and dozens of legumes and grasses are also subject to less direct insolation, and, in the case of the grasses, to less transpiration, because their leaves are plicate. Succulents, *e.g.*, *Asclepias* spp., *Euphorbia* spp., *Portulaca oleracea* L. and *Opuntia humifusa* Raf., occur in the sandhills, but they are also common on outer dunes, and other succulent species are characteristic of the salt flats of the maritime strand. A suggestive number of sandhill species, e.g., *Trichostema lineare* Walt., *Tragia urens* L., *Euphorbia gracilior* Ell., *Vernonia angustifolia* Michx., *Cassia nictitans* L., *Galactia regularis* (L.) BSP., *Hypericum gentianoides* (L.) BSP., *Lactuca graminifolia* Michx., *Gymnopogon brevifolius* Trin., and *Rynchospora grayii* Kunth, have narrower leaves than closely related species occurring in more mesic habitats.

Fire resistance is of considerable importance to sandhill species, and the prominent longleaf pine is noteworthy in this respect, "surviving fire (if not too intense) as no other tree in the region" (Wells & Shunk, 1931). A number of shrubs and small trees, by stolons or by suckers, sprout out rapidly after fires, increasing the scrubbiness of the flora. *Quercus* spp., *Myrica pusilla* Raf., *Rhododendron atlanticum* (Ashe) Rehd., *Amelanchier stolonifera* Wieg., *Robinia nana* (Ell.) Spach., *Rhus* spp., and *Vaccinium tenellum* Ait. are surculose species, probably capable of quick resurrection after fire. Laessle (1958a) points out that several species of the scrubs of Florida are vegetatively encroaching on the sandhills.

Geology

The Cretaceous, a period that witnessed a rapid evolution in the angiosperms, was a generally warm and mesic period. In that area now known as the Appalachians, an uplift presumably occurred, accompanied by a downward tilting of the coastal plain. This Cretaceous uplift initiated a vigorous erosion cycle, the coarse products of which were deposited as a blanket formation over the basement rock of the coastal plain. In places, this formation, the Tuscaloosa (Middendorf; Patuxent), is believed to be the direct or indirect source of the sands which make up the sandhills (Cooke, 1936; Heron, 1958). A map of the outcrop of the formation corresponds beautifully with a map of the fall-line sandhills. An equally striking correspondence is exhibited by the belt of sandy soil types paralleling the fall-line, the Norfolk and the Orangeburg soils.

Popular belief has long been that the sandhills represent dunes or deposits of an ancient sea. That the belt of sand parallels the sea has perhaps increased speculations that the sandhills represent Cretaceous dunes. These speculations are seriously weakened by the fact that the Tuscaloosa is a blanket formation, extending far from its outcrop belt along the fall-line to subsurface beds beneath and beyond the present shoreline, with an inner continental and an outer marine facies (Heron, 1958). Speaking of the surficial sands overlying the formation in the Carolina sandhill area, Heron (1958) says, ".... some of the sand undoubtedly is a part of the Middendorf (Tuscaloosa) Formation." Cooke (1936) says of the region of the Tuscaloosa outcrop in South Carolina, ".... throughout much of this area it gives rise to sandhills."

In North Carolina post-Tuscaloosa deposits are recognized in various areas but do not extend inland as far as the inner outcrops of the Tuscaloosa. Such deposits are the Black Creek formation, consisting of near-shore swamp and lagoonal deposits, and the Peedee formation, consisting mainly of glauconitic and calcareous sands.

Cooke's map (1945) of the Paleocene shoreline indicates that the sea again encroached almost to the fall-line. Richards (1950) doubts, however, that there were any major encroachments in North Carolina until mid-Eocene, when deposits were laid down locally as far inland as the fall-line. The local nature of these ferruginous deposits may be due to deposition by fingerlike extensions of a quiet sea, or to subsequent erosion. Eocene deposits of the inner coastal plain are much more common in South Carolina and Georgia, where they may result in reddish soils

of the Orangeburg type. The Eocene shoreline seems to be the only post-Tuscaloosa shoreline which could conceivably have been accompanied by dunes in the region of the fall-line sandhills, but the occurrence of marls (Richards, 1950) in the questionably Eocene deposits in North Carolina precludes any possibility of dune formation in conjunction with this Eocene sea.

The Oligocene invasion, so prominent in Florida, Alabama, and Georgia, apparently submerged very limited fragments of the Carolina coastal plain. Miocene produced three major invasions, none resulting in any deposits near the fall-line. Early Pliocene witnessed a slight marine encroachment in the southeastern states, with two possibly contemporaneous formations, the Waccamaw and the Croatan, deposited near the coast of North Carolina. Apparently none of these Oligocene, Miocene, and early Pliocene invasions directly affected the sandhill area.

Overlying the Tuscaloosa formation in some places is an unfossiliferous, nonmarine sand and gravel constituting the Citronelle formation, a formation of importance to the ecology of the fall-line hills. Berry (1919) assigned the formation to the Pliocene on the basis of negative fossil correlations (the type locality is fossiliferous), *i.e.*, no correlation with a Pliocene flora but an implied but poorly illustrated lack of correlation with a Pleistocene flora. Doering (1958) has re-evaluated Berry's data and points out that of fifteen species "presumed extinct" by Berry, seven were admittedly close to Pleistocene species, five were not specifically determined due to poor preservation, and only three were absent from later deposits. Doering has associated the Citronelle, formerly called the Lafayette formation in North Carolina (Stephenson, 1912), with an early Pleistocene renewal of tectonic activity resulting in renewed erosion and deposition. According to Doering, the Citronelle is lowest Pleistocene and pre-Nebraskan.

Stephenson (1912) says: "The terms sandhills has been applied to a series of rolling hills covering portions of Richmond, Scotland, Moore, Cumberland and Harnett counties, whose elevations vary from a little over 200 feet to perhaps 500 feet. In this region the comparatively thin and more or less discontinuous Lafayette (Citronelle) covering rests unconformably upon an eroded Patuxent (Tuscaloosa) surface, whose broader topographic features seem to correspond closely to the present surface topography."

Doering (1958) says: "... in the South Carolina coastal plain ... the Citronelle covers a hilly belt 50 miles wide. This belt extends from an eastward-facing escarpment at Orangeburg to a westward-facing escarpment at Leesville which overlooks the piedmont plateau region. ... The eastern boundary of the formation is an escarpment 50–100 feet high which extends for several hundred miles along the coastal plain; this escarpment is unquestionably a result of marine erosion—at its southern end it merges with the Trail Ridge—a marine bar which extends southward into Florida."

It seems that Doering regards the sandhills, usually associated with the Norfolk soils, and the red hills, often associated with the Orangeburg soils, as congeneric. That they are not is strongly suggested, especially in Georgia, where, as La Moreaux (1946) observes, "The Sand Hills represent the area in which the Tuscaloosa formation crops out in East-Central Georgia. These hills form a belt 2 to 8 miles wide along the northern margin of the Coastal Plain except where the Eocene deposits overlap the Tuscaloosa formation. At the place of this overlap the 'Red Hills' project across the Sand Hills to the Piedmont." It thus appears that the yellow fall-line sandhills are to be associated with the Tuscaloosa outcrop and the red hills with either the Eocene outcrop or the Citronelle formation.

That the Citronelle formation represents fluvial fans, which only locally overlie the Tuscaloosa outcrop, suggests that the sandhills are leached products of the Tuscaloosa formation, and that interfluvial portions of this outcrop have been available to plants since Cretaceous time.

Doering (1958) explains that the escarpment to the east of the Citronelle formation is a marine escarpment. He does not explain the escarpment, equally prominent, to the west of the sandhills. The fall-line sandhills are often conspicuously higher than the adjacent piedmont, with the result that the area of outcrop of the sediment is now higher than the region of the source. Three factors may be evoked to explain this anomaly:

1. Rarely are the porous sandhill soils subject to the sheet erosion which downgrades the adjacent clays of the piedmont. This introduces a pertinent hypothetical query: given equal hills of clay and sand under equal climatic conditions, which hill would be higher after a million years.

2. The fall-line sandhills are associated with a region of uplift. According to Fenneman (1938), "Continued uptilting of the landward edge of the

Coastal Plain has been considerably in excess of erosion." The deposition of the Citronelle is supposed to have been accompanied by crustal warping (Cooke, 1945).

3. Winds are supposed to have been especially strong to the south of glaciers (Flint, 1947), and wind still is an agent of redistribution in the sands, but it is not herein believed that the sandhills represent dunes.

The Pleistocene consisted of several drastic fluctuations of sea level. The Wisconsin glaciation, for example, tied up enough water to lower the present sea level by some 300 feet (Richards, 1950). The advance and retreat of the glaciers, reciprocated by retreat and advance of the sea level, is recognized to have occurred at least four times during Pleistocene. Many species with temperature-controlled distributions were probably confined to the southern portions of their present ranges during the glacial stages.

Cooke (1931) postulates seven Pleistocene marine terraces on the southeastern coastal plain, with the highest at around 270 feet above present sea level. Flint (1940, 1942) contests all but two of Cooke's shore lines. Flint recognizes only a wave-cut feature from 15 to 35 feet high, the Surry Scarp, with its toe at an elevation of around 100 feet, and a second, less conspicuous Suffolk Scarp, with its toe at an elevation of from 20 to 30 feet. Whether one accepts Cooke's maximum shore lines at 270 feet or Flint's at 100 feet, uniformitarian principles belie the Pleistocene formation of coastal dunes of the magnitude necessary to explain the altitude of the sandhills (over 800 feet in some regions of Georgia). Present dunes along the Atlantic Coast rarely exceed 100 feet in height. It seems safe to conclude that the sandhills do not represent coastal dunes formed in Pleistocene, nor did they receive any marine sediments in Pleistocene.

The sandhills are thus best regarded as discontinuous weathered remnants of the continental phase of the Tuscaloosa formation, parts of which have been available for plant occupancy since Tuscaloosa time.

Paleontology

Little is known of the ecology of a peneplain, but it seems a sound inference that arenicolous plants of the Cretaceous peneplain of the Appalachians must have been concentrated on the gruss of granitic monadnocks and on sandy fluvial terraces, if such are to be found in a peneplain. White (1945), referring to the present piedmont peneplain, says, "In general, the upland surface of the Piedmont is a peneplain which is very poorly developed along its western edges but shows increasing development to the east." Sandy terraces are rare indeed in the piedmont today. With the Cretacaeous uplift of the Appalachians, streams were rejuvenated and carried coarser loads, perhaps increasing the frequency of sandy fluvial terraces. It is not highly probable that this uplift was any more catastrophic than modern uplifts, so there was probably a continuum of habitats favorable for psammophytes.

Berry (1920) published a catalogue, based mainly on fossil leaves, of the Mesozoic flora of North Carolina. Ecological inferences drawn from fossil leaves are undoubtedly precarious. Scott (1954), working on Tertiary floras of Oregon, concludes, "The high percentage of extinct genera among Eocene plants known from fruits and seeds is in accordance with the suggestion that the leaves of some early plants may have differentiated along modern generic lines before their reproductive organs." The genera listed by Berry, based mainly on fossil leaves, are nevertheless occasionally referable to extant genera.

In Berry's list of over forty genera, the majority angiospermous, two elements were conspicuous, a temperate mesophytic element and a more tropical xerophytic element. Among the former element are such genera as *Magnolia*, *Liriodendron*, and *Sassafras* which today exhibit the familiar Asian-American disjunction. Among the more tropical elements are such genera as *Tumion*, *Ficus*, *Citrus*, *Manihot*, and *Myrsine*. This suggests that only species of more mesic temperate habitats were to span the Asian-American bridge, while more tropical xerophytic elements were in later periods to converge toward Florida. Fernald (1931) has emphasized the tropical affinities of the coastal plain flora as contrasted with the Old World affinities of the montane flora of the southeast.

Exposure of raw habitats, uplift of mountains, and, possibly, even overgrazing by large reptiles contributed to introgression and accelerated evolution by disturbing the rather stable habitats of the Cretaceous peneplain. With the advance of the Tuscaloosa Sea and the Mississippi Embayment, many plants were doubtlessly forced into the newly uplifted Appalachians and Ozarks, where mixing of floras and rigorous environmental selection, coupled with random fixation, all

probably contributed to the Cretaceous evolutionary burst.

Woodson (1947), in explaining the subspeciation of *Asclepias tuberosa* L., has called upon "Orange Island," a fluctuating archipelago in north-central Florida. Vaughan (1910) had concluded that Orange Island was above sea level throughout Cretaceous, and Woodson suggested that Orange Island might have been a third Cretaceous refugium, functionally equivalent to the Appalachian and Ozarkian uplands. There is as yet no decisive evidence for a land mass in the Orange Island area in Cretaceous. Cooke's maps (1945) indicate that portions of Florida were emerged as far back as early Miocene, perhaps again submerged in middle Miocene, and again emerged in late Miocene. Goin (1958) has presented rather striking herpetological evidence that there were Florida land masses available for occupancy as far back as early Miocene. James (personal communication, 1959) says, "... if Orange Island existed, it was less extensive than earlier believed, and could only have served as a refugium to the post-Eocene, the Early and Middle Oligocene life." The dichotomous radiation from northern Florida of the ranges of a great number of sandhill species certainly suggests that this archipelago, as a post-Cretaceous refugium, has been a focal point in the distribution, if not in the evolution, of the sandhill flora.

McVaugh (1943) has pointed out that members of the genera *Stipa*, *Aristida*, *Muhlenbergia*, *Xerophyllum*, *Zigadenus*, *Nolina*, *Eriogonum*, *Krameria*, *Psoralea*, *Petalostemon*, *Astragalus*, *Croton*, *Stillingia*, *Jatropha*, *Opuntia*, *Eryngium*, *Gilia*, *Penstemon*, *Hymenopappus*, *Brickellia*, and *Lygodesmia* are especially conspicuous in the fall-line sandhills. He adds that the eastern representatives are "... more or less isolated species belonging to genera which are most abundantly represented in western North America .... If it be granted that the area in which the flat-rocks occur has long been occupied by plants, it is but a step to the speculation that this same area may represent all or part of an ancient reservoir from which many species have attained their present ranges by radial spread." Doubtlessly many of these genera, and especially those genera of the longer available flat-rocks, such as *Talinum*, *Sedum*, *Schoenolirion*, *Nothoscordum*, *Yucca*, *Agave*, *Trifolium*, and *Hedyotis*, may have been represented in the east as far back as Cretaceous, but sandhill genera, with many western representatives and few eastern representatives, may have been of later appearance in the eastern flora. According to Dressler (1954), "During the Pliocene physiographic connections developed between the eastern United States and Mexico, but the middle Pliocene, at least, appears to have been a period of aridity (Axelrod, 1954), scarcely the proper setting for the southward extension of mesophytic plants." A rather sound corollary to this observation would be that the middle Pliocene did afford a proper setting for the eastern migration of xerophytes, many of which today may be present in the sandhills as derivatives of the Madro-Tertiary Geoflora.

Axelrod (1958) says,

> The Madro-Tertiary Geoflora had already appeared on the drier borders of the North American tropics by the Middle Eocene, and probably occupied much of the southwestern United States and adjacent Mexico by the close of the Oligocene. . . . The relationships of species of five types of vegetation in the fossil record—subtropical forest, deciduous hardwood forest, woodland, chaparral, arid subtropical scrub—thus unite to indicate that throughout the Tertiary there was a greater degree of similarity between the floras of the east and west coasts than exists today. . . . The Arizona chaparral also embraces species of *Acacia*, *Agave*, *Mahonia*, *Nolina*, *Fallugia*, *Mimosa*, and other genera that are not in the California community. . . . From the preceding discussion it is apparent that chaparral ranged across the present desert area in the Middle and Late Tertiary.

These statements suggest that certain genera of the western chaparral, an association also adapted to fire and prolonged drought, may have extended across to the eastern United States, perhaps via the Fayette sands of east Texas. Mid-Pliocene is the period most favorable for such an extension.

Forest (1935) has summarized concepts about the hypothetical Atlantean continent, a land mass supposed to have connected the eastern United States with Europe. Cooke (1945) suggests that if this continent existed, it would have been bounded to the south by a coastal plain, and it would have been arid during Pliocene. There is no support for the Atlantean hypothesis in the sandhill flora. Should there have been such a continent, a strong similarity should be expected between the xerophytic floras of the eastern United States and Europe. Analysis of the species of fixed dunes of England, as compiled by Salisbury (1952), reveals few specific con-

tinuities with the sandhills other than those of such weedy species as *Rumex acetosella* L., *Plantago lanceolata* L., and *Achillea millefolium* L.

Geography

The most striking feature of the distribution of the sandhill flora is that many of its elements range about equidistantly to the west and northeast from Florida. Phrases such as "Fla. to Ga. & Ala.", "Fla. to Miss. & N. C." and "Fla. to Tex. & N. J." recur monotonously in the range citations of sandhill species, and strongly suggest equilateral radiation or reradiation from Florida. As early as 1906, Harper was apparently also impressed by these distribution patterns:

> In range the sand-hill plants are more restricted than those of dry pine-barrens. Those peculiar to the sand-hills are nearly all confined to the coastal plain, and conversely, those whose ranges cross the fall-line nearly all occur also in dry pine-barrens. Most of the characteristic sand-hill plants do not range farther north than North Carolina or farther west than Mississippi.

Fernald, taking offense at Harper's omission of Virginia, launched a series of excursions, extending the ranges of over 115 sandhill species into Virginia. Then Fernald (1937) offers a useful, but somewhat Ptolemaic, Virginia-centered classification of the distribution patterns of the floral elements of the southeastern coastal plain. It becomes rather obvious that a Florida-centered classification is far more meaningful and natural when sandhill species are considered.

Small (1933) lists over 950 species as occurring in sandhills, scrubs, pinelands, or dunes. Of these, more than 90 per cent occur in Florida, with almost 450 endemic to Florida. Less than 10 per cent have extended up the Mississippi Valley as far as Arkansas. Several of those that do reach up the valley are frequent in the dunes of the Great Lake region and in the sands of the New Jersey pine barrens, and these species are not at all confined to the coastal plain in the states herein studied, but freely pass into xeric soils of the piedmont and lower mountains.

For those not extending up the Mississippi Valley, a numerical expression has been applied to facilitate an evaluation of the distributions. Using Florida as a center, a value of *1w* has been assigned to species ranging west to Alabama and no farther; a value of *2w* to those ranging west farther than Alabama but no farther than the Mississippi River; a value of *3w* to those ranging from Florida west across the Mississippi. For the northeastward extension, a value of *1e* has been assigned to species ranging as far as Georgia but no farther; a value of *2e* to those extending farther northeast than Georgia but no farther than southeastern Virginia; a value of *3e* to those ranging from Florida farther northeast than southeastern Virginia. Coupling the westward value with the northeastward value yields the numerical expression for the distribution of a species; *e.g.*, a species with a distribution of Florida to Alabama and Georgia would bear the designation *1w–1e*; a species ranging from Florida to Texas and North Carolina would receive the designation *3w–2e*; a species ranging from Florida to Maryland would bear the designation *0w–3e*.

Applying these designations to the psammophytic coastal plain species derived from Small (1933) yielded the following results: *2w–2e*, 70 spp.; *0w–2e*, 49 spp.; *0w–1e*, 40 spp.; *0w–3e*, 4 spp.; *1w–3e*, 1 sp.; *1w–2e*, 23 spp.; *2w–3e*, 12 spp.; *2w–0e*, 26 spp.; *1w–0e*, 16 spp.; *2w–1e*, 23 spp.; *3w–1e*, 8 spp.; *3w–0e*, 21 spp.; *3w–2e*, 43 spp.; *1w–1e*, 20 spp.; *3w–3e*, 10 spp.; endemic west of Florida, 10 spp.; endemic northeast of Florida, 41 spp.; endemic in northern Florida, 55 spp.; and endemic in peninsular Florida, 388 spp. These figures are diagrammatically presented in Table II.

The totals presented in Table II indicate that there is no strong eastern or western disposition of the flora, but rather that the flora is almost equally divergent from Florida, thus strongly suggesting that, at some time, it has been confined to Florida. Endemics occurring only west of the Mississippi River or north of Virginia have not been considered. The somewhat higher endemism to the northeast of Florida than to the west tends to support the contention that the fall-line sandhills have been longer available to plants than the sand ridges to the west. Were the northeastern endemics subtracted, there would be a slightly greater western than northeastern total (see Table II). This may perhaps be attributed to the postulated Pliocene advent of Madro-Tertiary elements.

The distributions of those species not confined to Florida embrace at least five categories:

1. **Local Endemics.** Among these must be considered such plants as *Elliottia racemosa* Muhl., formerly known from only a few stations in Georgia and South Carolina but now almost extinct, and *Pyxidanthera barbulata* var. *brevifolia*

Table II

Distribution of psammophytic coastal plain species

	3w	2w	1w	Fla.	1e	2e	3e	
Equilateral Distribution	5	35	10	N. Fla. 55	10	35	5	Equilateral Distribution
Farther West	51	23				23	13	Farther Northeast
Strictly Western	21	26	16		40	49	4	Strictly Northeastern
Endemic West of Florida		10				41		Endemic Northeast of Florida
				Pen. Fla. 388				
Total "Western" Species = 197				Total Florida Species = 443				Total "Northeastern" Species = 220

(Wells) Fern., apparently relict to one county in North Carolina, where it is persisting through vegetative activity alone (Wells & Shunk, 1931).

2. **Recently Adventive Pioneers.** Here may be cited *Wahlenbergia marginata* (Thunb.) A. DC. and *Striga asiatica* O. Kzte., recently adventive arenicolous species, which may soon spread out to occupy the entire range of the longleaf pine.

3. **Recently Spreading Pioneers.** Probably an excellent example of this category is *Chrysopsis pinifolia* Ell., originally known only from Georgia, now spread to North Carolina, where it is locally abundant. In Wayne County, North Carolina, perhaps its present northern limit, this is the most conspicuous herbaceous species over acres of burned-over pineland. Although local in its distribution, this species, where found, gives the impression of an aggressive weed.

4. **Reradiated or Reradiating Relics.** The majority of the nonweedy sandhill species probably belong to this admittedly ambiguous category. These species occupy the belt of the longleaf pine or portions of it, and presently seem to be rather static in their distributions. Here belong such species as *Chrysoma pauciflosculа* Greene and *Ceratiola ericoides* Michx. *Chrysoma*, ranging from Florida to North Carolina, was formerly in South Carolina known at only one station, in Lexington County, but Terrell (1958) reports finding it in Robeson County, North Carolina, 125 miles northeast of its former northernmost station. *Ceratiola* reaches its northern limit in Kershaw County, South Carolina—that is, as far as the fall-line sandhills are concerned. This species, like so many species, and probably all those species reaching their northern limits in southeastern Virginia, usually occurs farther north along the outer scarps and ridges than in the fall-line sandhills. Many northern limits are temperature controlled, and plants nearer the ocean would have the benefit of the oceanic amelioration of the climate. The category "reradiating relics" implies that these species were quite possibly confined to Florida or vicinity during the last glacial era as relics and have reinvaded their former areas as pioneers in the present interglacial epoch. In the absence of a complete fossil record and reliable archives, reference to the relic or pioneer category is largely guesswork, except in those cases where the species is no longer capable of producing propagules.

5. **Pioneers to or from the Appalachian Upland.** Many species may have migrated across the fall-line during various geological eras. Such species may now have scattered isolated colonies in the mountains, where there are savannalike habitats. Of limited occurrence in these mountain "savannas" and more frequent occurrence in the coastal savannas are such genera as *Amianthium*, *Xerophyllum*, *Helonias*, *Cleistes*, and *Calopogon*. Controversy exists over these disjunctions.

Fernald (1937) believes them to be relict in the mountains since Cretaceous. Pennell (1935), on the other hand, suggests that the orchids, at least, might represent post-Cretaceous pioneering invaders of the mountains. Whether they represent relics or pioneers, it is very doubtful that they have occupied the same ranges since Cretaceous.

Of several xerophytic sandhill species which freely cross the fall-line, many are found in the stable dunes of the Great Lakes region and in the high pine barrens of New Jersey. The unstable dunes of the Great Lakes region seem to be ecologically governed by the wind, and it is only the stable dunes which show pronounced floristic affinities with the sandhills. These sentiments are well expressed by Cowles (1899), speaking of the Lake Michigan dunes: "The flora of the oak dunes, especially that found on sunny southern slopes, is a true xerophytic flora, but a xerophytic flora resembling that of the more southern type, where the adaptations are developed to protect against heat and transpiration which it causes .... The oak cannot get a foothold until the dune has become well established and protected from the lake winds .... On the southern slope, where there is continuous exposure to the sun, there is rarely a continuous vegetation carpet, but a more or less tufted vegetation with intervening patches of naked sands."

Phytosociology

Wells and Shunk (1931), working in the fall-line sandhills of Harnett County, North Carolina, have divided the flora of the coarse inland sands into the following: (1) Quercus-Aristida Associes, Pioneer Stage; (2) Xeric Phase, Aristida Consocies; (3) Xero-mesic Phase, Aristida-Quercus (marilandica) Mictium; (4) Mesic Phase, Aristida-Hicoria Mictium; and (5) Semi-hydric or Semi-bog Phase, Aristida Consocies of the Campulosus-Panicum Mictium. Where no subsurface irregularities occur, these phases are occasionally recognizable in a transect from the top of a sandhill to the edge of a pocosin. The five phases of Wells and Shunk are characteristic of those habitats normally above the water table in the sandhills and constitute three of the five intergrading habitats common in the fall-line sandhills. These five common habitats, presented schematically in Diagram 1, have been given different names according to the dominance of angiosperms or gymnosperms.

For those habitats above the water table, the

TURKEY OAK BARREN	
(Dry Pineland)	
SCRUB OAK BARREN	
(Intermediate pineland)	
SAVANNA	
(Low pineland)	
water table	
nonalluvial	*alluvial*
SHRUB BOG OR BAY	SWAMP FOREST
(Pocosin)	(Cypress Swamp)
(White Cedar Bog)	

DIAG. 1: Schematic presentation of the commonly occurring habitats of the fall-line sandhills

angiospermous and gymnospermous contingents at a given level are believed to be consocies in accordance with the first, third, and fifth of the criteria set up by Gleason (1910): "Two areas of vegetation dominated by different species are accordingly probably consocies of the same association (1) if there is no obvious difference in the environments; (2) if there is no evidence of succession between them; (3) if the secondary species are the same for each; (4) if the dominant species are of the same vegetative form or (5) tend to mingle in other areas with the same environment and secondary species." As for succession (second criterion), in this case a questionable issue, it seems plausible from historic inferences and field observations that, if man had not largely removed the longleaf pine as a seed source, the xerophytic oaks would give way to the longleaf pine, in antithesis to the expected pine-oak trend normal in the piedmont. The high incidence of fire would preclude the possibility that the pines would give way to the climax oaks of the piedmont.

I. Turkey Oak Barren (high pineland): Dry acid sands, not subject to salt spray, dominated by the turkey oak or the longleaf pine, with the water table usually more than four feet below the surface. This habitat would embrace the first and second phases of Wells and Shunk (1931). Harper (1906) defines pine barrens as "the forests in which *Pinus palustris* is more abundant than all other arborescent species combined, and the trees do not grow thickly enough to sensibly diminish the quality of light which reaches the ground." This is a useful inclusive term, for it embraces the high, intermediate, and low pinelands, many of which have been con-

verted into oak barrens and savannas by exhaustive lumbering. North of southeastern Virginia and south of north-central Florida, the longleaf pine is replaced by other pine species.

II. Scrub Oak Barren (intermediate pineland): Dry acid sands, not subject to salt spray, dominated by species of oak (as *Quercus incana* Bartr., *Q. marilandica* Muenchh. or *Q. margaretta* Ashe) or pine (usually *Pinus australis* Michx., but other species are more frequent here than in the turkey oak barrens), with the water table usually one to four feet beneath the surface. This habitat would embrace the third and fourth phases of Wells and Shunk (1931). Scrub oak barrens are slightly more mesic than turkey oak barrens and are frequently below them on hillsides. They support a slightly wider variation of herbs, a greater proportion of which also occur in the sterile oak-hickory woods of the piedmont and mountains. Due to decreasing relief, scrub oak barrens are of increasing frequency towards the coast. In such barrens are increasing quantities in species of *Ilex*, *Myrica*, *Vaccinium*, and *Gaylussacia*. Hilgard (1860) must have felt similarly a century ago in Mississippi when he wrote: "The farther we advance southward the more numerous various species of Huckleberry and Whortleberry . . . are represented in the undergrowth and in the same manner the Gallberry and Candleberry increase in a southward direction until, near the sea coast, they become very abundant." This tends to introduce the hypothetical concept herein suggested that, in crossing sand ridges from the innermost sandhill to the outermost stable dune, the sere turkey oak barrens-scrub oak barrens-maritime forests transition is ideally to be expected.

Harper (1905) attempted to clarify the etymology and orthography of the word *hammock*. Laessle (1942) defines a hammock as a predominately broad-leafed evergreen association of trees growing on soils seldom if ever subject to flooding. This definition would not exclude the maritime forest of the Carolinas and the two—hammock and maritime forest—share many species. For those who wish to separate them, the phrase "and not subject to salt spray" should be appended to the definition of the hammock. There is question of their distinctness even in Florida, for Kurz (1942) refers to the maritime forest as hammock. Although the maritime forest species of Florida are of rather widespread occurrence in non-coastal hammocks there, those few that reach the Carolinas are often closely restricted to the maritime strand.

Laessle (1958a) has noted the affinity of some Florida scrub species with some of those of the hammock. The occurrence in the Florida scrub of species which are closely restricted to the maritime forest in the Carolinas may throw some doubt on the idea that the scrub is more sterile than the sandhills of Florida. Laessle, in an excellent comparative study of scrubs and adjacent sandhills, has concluded that the scrub soils are more thoroughly worked by the depositing agents, and hence more sterile, than the sandhill soils.

A few of the species that Laessle (1958a) lists for the Florida scrubs and sandhills also occur in the sandhills of North Carolina, and several of those were mentioned by Wells and Shunk (1931) in various phases of the Carolina sandhills. The largest number of the scrub species listed by Laessle that also occur in the lists of Wells and Shunk are to be found in their mesic phase. Conversely, the largest number of the sandhill species listed by Laessle that also occur in their lists are in their xeric phase. From this it would seem that the Florida scrub is slightly more mesic than the Carolina turkey oak barren and perhaps pedologically more closely related to the scrub oak barren. In the fall-line sandhills, the differences between turkey oak barren and scrub oak barren are probably determined by water relations. The differences between the Florida sandhill and scrub might conceivably be similarly explained. The following reasons tend to suggest this.

1. Analysis of the topographical descriptions of the scrubs presented by Laessle (1958a) reveals that the majority of them, *e.g.*, the scrub at Keystone Heights, Goldhead State Park, the Lohman Scrub, the Ocala National Forest Complex, the Big Scrub, and the Altoona Scrub, are adjacent to sandhills of higher elevations. Of those scrubs not exceeded by sandhills, most are those which he terms hilltop scrubs, which are ocean-beveled hilltops covered by layers of sand. In such situations, peculiar drainage conditions might account for the presence of scrubs. In North Carolina, scrub oak barrens at the top of a sandhill indicate a clay subsoil. According to Wells and Shunk (1931), "Every countryman in such regions knows that black jack oak, when found on the tops and upper slopes of hills, indicates a clay subsoil."

2. Laessle (1958a) notes that the species of the scrubs have a greater affinity with species of the

hammock than of the sandhills. Hammocks are unquestionably more mesic than scrubs. The closer floristic affinity of the scrubs with the hammocks than with the sandhills suggests that the scrubs are more mesic than the sandhills.

3. Laessle (1958a, 1958b) reports the encroachment of scrub species on sandhills and interprets that the scrub species are vegetatively crowding out the shade-intolerant sandhill species. An alternative interpretation worthy of consideration is that water relations have improved enough to influence the vegetation.

4. *Rhynchospora dodecandra* Baldw., cited by Laessle (1958a) as an indicator species of the scrub, is rare in the turkey oak barrens of the fall-line sandhills, but is less rare in more mesic habitats. This is also true of some other species found in his scrub list.

5. Harper (1906) noted the affinity of his sand-hammock species with the Florida scrub. Analysis of the species listed for the sand-hammock indicates that it is a phase of the Altamaha Grit region closely analogous with the mesic phase of Wells and Shunk (1931). The sand-hammock shares many species with the scrub and some species with the mesic and xero-mesic phases of Wells and Shunk.

The evidence in this issue is by no means unilateral. The following points, which suggest that the scrubs are less mesic or fertile than the sandhill, are problematical and could be clarified by accumulation of enough pertinent data.

1. In the Carolinas, *Quercus incana* Bartr., *Q. marilandica* Muenchh., and *Q. margaretta* Ashe indicate more mesic conditions than does *Q. laevis* Walt. Although none of Laessle's (1958a) lists of scrub species contain the more mesophytic oaks, the turkey oak appears frequently. That the mesophytic oaks are lacking and the turkey oak is present suggests that the Florida scrubs are more xeric than the Carolina scrub oak barrens, or that the scrubs contain elements antagonistic to the mesophytic oaks. An analysis of sandhills and scrubs in northern Florida, with emphasis on oak composition, should be illuminating.

2. Laessle (1958a) weighs the data from soil analyses as suggesting that the scrub soils are perhaps more xeric and sterile than the sandhill soils. The analyses to which he refers do indicate the nature of the soil but generally fail to indicate the depth of the water table. The coarsest of sands, although superficially dry, may support mesophytic species, if shallowly underlain by the water table or hardpan. The difficulty of obtaining data on the water table may defer the outcome of the debate. It is to be hoped that citrus experiment stations will make careful notes on the previous natural vegetation in their studies of the water table, which is so critical in the citrus industry. Killing of citrus roots resulted from an unusually high water table, 2.8 to 0.9 feet below the surface during the period from July to October in 1954, when rainfall of at least nine inches each month fell in portions of Florida. The average water table in the area studied was four feet below the surface (Reitz & Long, 1954).

III. Savanna (low pineland): Periodically dry acid sands, not subject to salt spray, dominated by grasses or pines, with the water table or hardpan usually within one foot of the surface. This would embrace the semihydric phase of Wells and Shunk (1931). Savannas, depending on the relief, occur as narrow or broad ecotones between the oak barrens and the shrub bogs. Savannas are generally believed to be fire initiated and fire maintained. The idea that savannas are initiated from shrub bogs by fire in an unusually dry season (Wells, 1942) is problematical, for a fire would lower the soil surface somewhat, after gaseous products had been dispersed, in effect raising the water table.

Savannas are of limited occurrence in the sandhills, and, due to extreme relief, are usually confined to narrow ecotonal strips between the barrens and shrub bogs. Where hardpans and argillaceous formations intersect the surface in the sandhills, small seepage savannas often develop which support a flora identical with the extensive savannas of the low country. It is quite probable that these ecotonal and seepage savannas in the fall-line sandhills were the first savannas available for plant occupancy after the Cretaceous inundation. Whether fire was as frequent then as today is conjectural, but presently "the number and severity of fires is greater in sandhill vegetation than in any other vegetation" (Wells & Shunk, 1931). If post-Tuscaloosa fires were common, as the frequency of charred fossils suggests, many of the elements of the flora of the vast savannas of the coastal terraces may have originated in the ecotonal savannas of the sandhills.

IV. Shrub Bog; Bay (pocosin; white cedar bog): Usually wet or inundated peaty sands, not subject to salt spray, with little increment of alluvium, dominated by evergreen shrubby angiosperms or gymnosperms (especially *Pinus*

serotina Michx. or *Chamaecyparis thyoides* (L.) Britt.). These occur in local closed depressions and along small streams carrying or depositing little alluvium. The elliptic evergreen leaves, monotonously recurrent in the shrub bog flora, have long been a source of curiosity.

V. Swamp Forest (cypress swamp?): Usually wet or inundated argillaceous sands, not subject to salt spray, with a heavy increment of alluvium or organic matter, dominated by angiosperms (especially *Nyssa* spp.) or gymnosperms (*Taxodium* spp.). Normally the swamp forests occur in the sandhills only where the larger streams have formed flood plains. The cypress swamp, commonly associated with streams originating in the coastal plain and laden with organic matter rather than with silt, is rarely developed naturally in the fall-line sandhills but may be found in artificial empoundments. Cypress ponds are frequently surrounded by shrub bogs.

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Endosperm Development and Associated Ovule Modifications in the Genus *Ilex* L.[1]

J. M. Herr, Jr.
Department of Biology, University of South Carolina, Columbia, S. C.

The report presented here follows from the study of ovule development and megagametogenesis in *Ilex* L. reported by Herr (1959) and similarly treats of six species in the principal subgenera *Euilex* Loes. and *Prinos* (L.) Loes. The species selected fairly represent the genus and should exhibit the range of variation in endosperm development and associated structural changes in the ovule. The early phases of endosperm development, showing considerable variation within a species, have been studied most extensively in *Ilex opaca* Ait. Studies of the early phases in *I. crenata* Thunbg., *I. cornuta* Lindl. & Paxt., *I. verticillata* (L.) Gray, and *I. decidua* Walt. are somewhat less complete. Suitable fixation of these early phases has not been attained for *I. vomitoria* Ait. All six species show marked similarity in the structure of the mature endosperm.

These observations are compared with those reported by Schürhoff (1921) for *I. aquifolium* L. and with those from related Celastraceae treated by Andersson (1931).

Materials and Methods

Pistillate flowers used in this study were collected after full anthesis during May and early June over a period of several years. Vouchers for these collections, deposited in the University of North Carolina Herbarium, have been cited in the previous paper.

Adequate fixation of all material (except *I. vomitoria*) was achieved with several fluids, but FPA 50 (formalin-propionic-50% ethyl alcohol) proved most reliable. Fixatives prepared as recommended by Johansen (1940) were applied at the time of collection.

All material prepared for sectioning was dehydrated by the tertiary butyl alcohol method and embedded in paraffin. Longitudinal sections 12–15 μ in thickness from whole ovularies or individual ovules proved most useful for all stages of endosperm development.

Adequate staining was achieved by the application of safranin and fast green as recommended by Johansen (1940) and by alteration of this technique described by Herr (1959).

The magnification of each photograph and camera lucida drawing is cited in the legends.

Magnifications cited earlier by Herr (1959) are partly in error. Figures 1 through 21, for which magnifications of either ×53, ×67, or ×100 are given, are actually magnified ×40, ×50, or ×75 respectively. Figures 86 and 87 given as ×267 are actually magnified ×116.

Observations

In all species studied, endosperm development reaches an advanced stage prior to the initial phase of embryogeny, namely, the transverse division of the zygote.

Division of the primary endosperm nucleus in *I. opaca* follows closely upon triple fusion (Fig. 1). Formation of a transverse wall between the daughter nuclei establishes two endosperm chambers. The micropylar chamber is consistently larger than the chalazal one (Fig. 3). Subsequent events show some variation, but usually the division of both endosperm nuclei is simultaneous. The micropylar nucleus divides in the horizontal plane, and the division of the chalazal nucleus is vertical (Fig. 4). These division figures are parallel to the median longitudinal plane of the anatropous ovule, *i.e.*, a plane passing through the funiculus and the main body of the ovule. Formation of a vertical wall between the chalazal nuclei usually precedes

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the establishment of a horizontal wall in the micropylar chamber (Figs. 5 and 6). The endosperm thus develops three chambers in linear sequence, the chalazal one of which contains two cells. The antipodal cells frequently persist throughout the early stages of endosperm development. In some instances, the egg or zygote nucleus is observed in close association with one or two sperm cells (Fig. 2). Apparently more than one pollen tube may enter the same ovule. Nuclear division in the vertical plane occurs in the central chamber and is followed by the formation of a vertical wall (Fig. 7). Similar divisions occur later in the micropylar nucleus and in each of the chalazal nuclei. However, the division figures of the chalazal nuclei are perpendicular to the longitudinal plane of the ovule. The subsequent formation of vertical walls produces eight cells in the secondary endosperm, four in the chalazal chamber and two each in the central and micropylar chambers (Fig. 8). After the central and micropylar chambers are each partitioned into four cells, the further divisions in the endosperm are various as to time and place of occurrence. Consistently, however, the rate of cell division is greater in the micropylar and chalazal regions than in the central portion.

The second division in the endosperm often occurs first in the micropylar nucleus, and the formation of a transverse wall establishes three unicellular chambers. Division of the chalazal nucleus soon follows, and development continues as previously described (Fig. 9).

In many instances, the micropylar nucleus divides first in the vertical plane. Formation of the vertical wall prior to division of the chalazal nucleus establishes three cells in the secondary endosperm (Fig. 10). The division of the chalazal chamber follows in the usual manner to produce the four-cell stage, and in some instances the four nuclei divide simultaneously (Fig. 11).

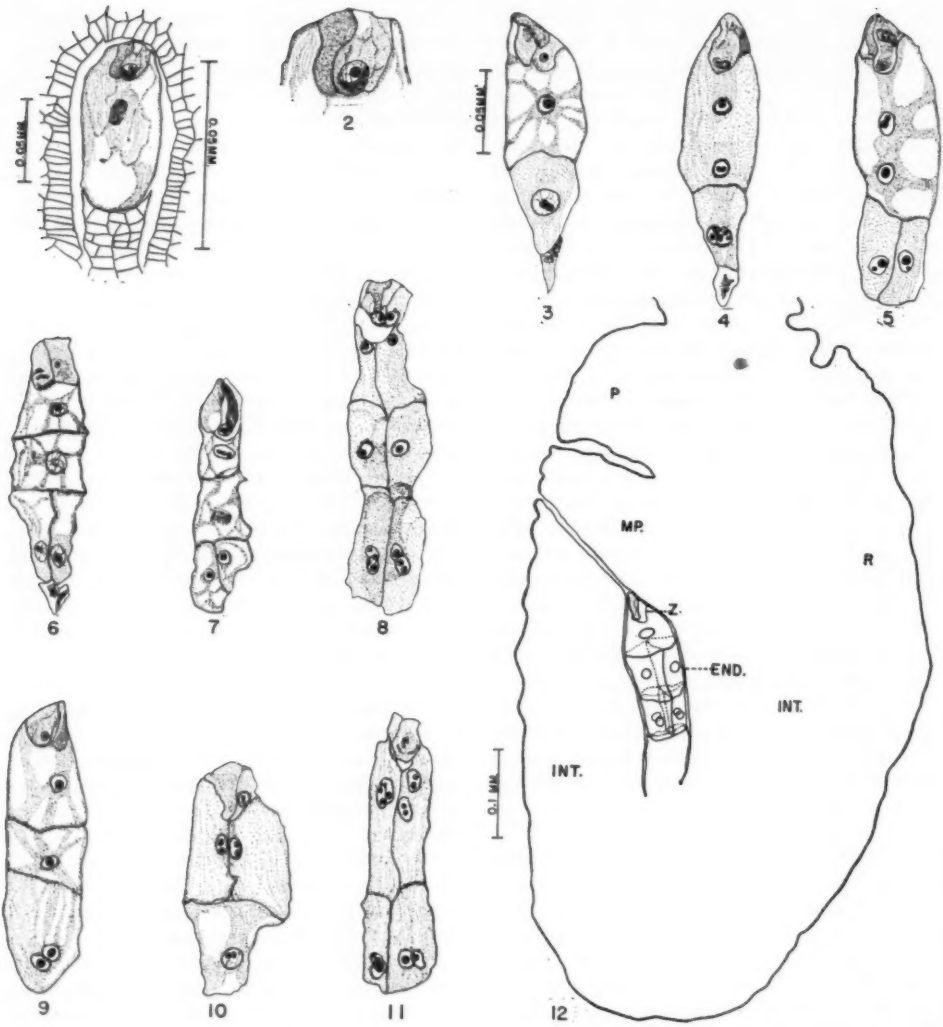
It is clear from these observations that the young endosperm of *I. opaca*, which exhibits the several variations in form just described, occupies a characteristic position within the anatropous ovule. The primary endosperm is first partitioned to form a secondary endosperm with a chalazal chamber and one or two micropylar chambers in linear sequence. Two vertical divisions produce four cells in each chamber, two toward the side of the ovule on which the micropyle opens and two on the opposite side toward the raphe (Fig. 12). These vertical divisions usually occur first in the chalazal chamber.

The zygote remains relatively unchanged throughout the early stages of endosperm development, but it begins to elongate when the endosperm reaches the multicellular stage.

Throughout the early stages of endosperm development, the ovule enlarges and the epidermis undergoes further differentiation (Herr, 1959). The cell walls become thickened, but the exact nature of the thickening material is not known. Ives (1923) reports both suberin and mineralized lignin in the epidermis of mature seeds. Initial differentiation of the inner cell layer of the integument occurs to establish the tapetum. It is marked chiefly by the radial elongation of the cells and the appearance of dense cytoplasm. These initial changes occur in uniform degree from the chalazal to the micropylar region of the ovule (Fig. 13).

A small group of cells at the apex of the integument often becomes lignified during the early stages of endosperm development. These cells occur predominantly in the region immediately adjacent to the funiculus (Fig. 14). Lateral illumination of the ovule reveals that druses occur abundantly in the general region marked by lignification (Fig. 15). Ovules with young endosperm often show a complete absence of this phenomenon (Fig. 13). On the other hand, it is occasionally evident in ovules that contain the mature megagametophyte. Distinct enlargement of the funicular protuberance has accompanied the other changes here described (Figs. 13, 14, and 15; *cf.* Figs. 1–3, Herr, 1959).

During the advanced development of the endosperm, the ovule undergoes marked elongation. Subsequently, differentiation in the epidermis appears uniform over the entire surface. Further differentiation of the tapetal layer, involving more intense staining of the cell walls and nuclei, the occasional binucleate condition, and the general presence of particulate cytoplasm, appears first in the chalazal region and progressively diminishes toward the micropyle (Figs. 16, 17, and 18). The funicular protuberance does not show marked growth, and frequently the apical region of the integument is only slightly lignified (Fig. 16). In many instances, however, lignification of this region is quite pronounced and is often extended around the entire circumference of the ovule (Fig. 18). Lateral illumination shows abundant druses in the region occupied by lignified cells. The lateral distribution of the druses toward the chalaza mark out the general region in which future lignification will occur (Fig. 19).



FIGS. 1–12. *Ilex opaca* Ait. FIG. 1. Primary endosperm nucleus at telophase. ×250. FIG. 2. Egg or zygote nucleus in close association with sperm cell. ×567. FIG. 3. Two chambers in secondary endosperm; micropylar chamber larger than chalazal one; distorted antipodal cells present. ×250. FIG. 4. Each chamber binucleate as result of vertical division of micropylar nucleus and horizontal division of chalazal nucleus. ×250. FIG. 5. Vertical wall formation establishes two cells in chalazal chamber. ×250. FIG. 6. Completion of division in micropylar chamber establishes three linear chambers in secondary endosperm. ×250. FIG. 7. Nucleus of central chamber at telophase in horizontal plane. ×250. FIG. 8. Two cells in each micropylar chamber; four cells in chalazal chamber. ×250. FIG. 9. Second division of endosperm advanced in micropylar chamber to establish three linear, unicellular chambers. ×250. FIG. 10. Early vertical division of micropylar chamber forms three cells in secondary endosperm. ×250. FIG. 11. Second division vertical in both chambers; synchronized third division establishes eight nuclei, finally eight cells in secondary endosperm. ×250. FIG. 12. Diagrammatic outline of typical *Ilex* ovule sectioned to show position of young endosperm (END.) of seven cells in relation to integument (INT.), micropylar passage (MP.), funicular protuberance (P), and raphe (R). c. ×133.

In *I. crenata*, the division of the primary endosperm nucleus and the establishment of two endosperm chambers follows precisely the pattern observed in *I. opaca*. Frequently, the chalazal endosperm chamber is enclosed by nucellus. This unusual condition suggests the persistence of the nucellus lateral to the mature megagametophyte, but it may result from growth of the endosperm downward to a greater depth in the basal nucellus. Other stages in the early development of the endosperm have not been observed. The multicellular form achieved is very similar to that found in *I. opaca*.

The ovule continues to enlarge throughout megagametogenesis. During the early development of the endosperm, differentiation of the outer layer in the chalazal region increases and may be extended to a few epidermal cells in the lower portion of the raphe. The tapetal layer is differentiated and frequently appears more distinct here than in *I. opaca*. In most instances, the funicular protuberance becomes more distinct, but it does not attain the prominence reached in other species (Fig. 20).

During advanced endosperm development, the ovule enlarges but otherwise shows few changes. In most respects, the tapetal layer is similar to that of *I. opaca*. Lignification is initiated at the apex of the integument but never becomes as extensive as in the other species (Fig. 21).

The two-chambered secondary endosperm in *I. cornuta* forms in the usual manner, but it appears less elongate than in the other species. Subsequent divisions have not been observed. A multicellular endosperm developing prior to elongation of the zygote was seen in several preparations.

Only minor changes in the structure and form of the ovule occur during the advanced stages of endosperm development. The cells in the epidermal layer of the integument are much smaller than those of the other species, but they undergo a similar pattern of differentiation. Lignification in the apex of the integument is scanty. In most instances, the tapetum shows complete absence of the distinctive secondary features which characterize its development in the other species (Fig. 22).

None of the early stages in endosperm development have been observed in *I. vomitoria*. The general form of the advanced endosperm and the behavior of the zygote follows the typical pattern.

Lignification in the apex of the integument usually occurs with the advanced stages of endosperm formation and is confined to the micropylar region. Druses occur abundantly at the apex and extend also to the lateral regions adjacent to the endosperm (Fig. 23).

In *I. verticillata*, division of the primary endosperm nucleus is followed by the typical formation of the two-chambered, secondary endosperm. The second division follows the usual pattern to originate three chambers. In some instances, the micropylar nucleus divides in the horizontal rather than the vertical plane ultimately to establish four chambers in linear sequence. Subsequent divisions vary, but generally the development of the multicellular endosperm and behavior of the zygote follow the pattern described previously for *I. opaca*.

During the early stages of endosperm development, the ovule continues to enlarge while the epidermis differentiates progressively from the chalaza toward the micropyle. Frequently, however, differentiation occurs well in advance of this general progression in groups of cells which are located in the lower portion of the raphe and in the micropylar region of the integument (Fig. 24).

Division of the primary endosperm nucleus and the formation of two chambers follows the typical pattern in *I. decidua*. Other early divisions have not been observed, but three chambers form in the endosperm prior to the onset of vertical divisions.

During the early stages of endosperm development, lignification is quite evident in the apex of the integument. It occurs most abundantly in the region immediately adjacent to the funiculus (Fig. 25). In ovules which show elongation of the zygote, lignification is still confined to the region immediately adjacent to the micropylar passage (Fig. 26).

Discussion

The early development of the endosperm in *Ilex* conforms to the pattern referred to as the Cellular type. Formation of three chambers in linear sequence is considered characteristic here, and most deviations from this pattern are probably insignificant. The principal variation in *I. opaca*, however, in which only two chambers are formed prior to the onset of vertical divisions, might effectively reduce the total length of the endosperm mass. Perhaps this variation is

FIGS. 13–26. *Ilex opaca* Ait. FIG. 13. Early endosperm development; differentiation in epidermis; initial differentiation in integumentary tapetum. ×50. FIG. 14. Early endosperm development; lignification in apex of integument, predominantly in region adjacent to funiculus (L). ×50. FIG. 15. Ovule of Fig. 14; lateral illumination reveals abundant druses in region of lignification. ×50. FIG. 16. Advanced endosperm; growth of funicular protuberance slight; secondary differentiation in tapetum progressive from chalazal to micropylar region; apical lignification slight (L). ×50. FIG. 17. Advanced endosperm; cells of tapetum (T) show darkly stained cell walls and nuclei, typical of secondary differentiation. ×175. FIG. 18. Advanced endosperm; lignification in apex of integument extends around circumference of ovule. ×50. FIG. 19. Ovule of Fig. 18; druses occur abundantly in region of lignification; their lateral distribution coincides with region of later lignification. ×50. FIGS. 20–21 *Ilex crenata*. Thunbg. FIG. 20. Early endosperm development; ovule enlarges uniformly; differentiation of chalazal epidermis and

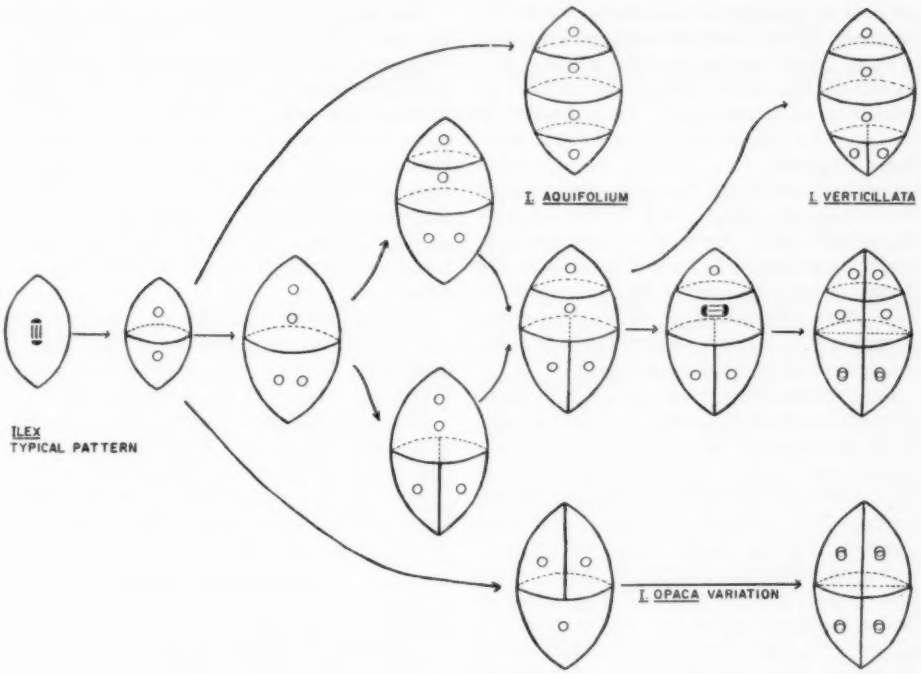


DIAGRAM 1.

associated with the frequent production of small seeds noted by Barton and Thornton (1947).

Schürhoff (1921) reports that in *I. aquifolium* four endosperm chambers are formed prior to the onset of longitudinal cleavages. Formation of four chambers has been observed here only in *I. verticillata*, but in this case the micropylar chamber in the series may have been formed subsequent to vertical division of the chalazal chamber. All of the variations in early endosperm development observed and discussed here and their relationship to the typical pattern are summarized in Diagram 1.

Schürhoff also states that the nucellus is displaced by endosperm formation. The statement may refer to the disintegration of the basal nucellus in connection with the downward extension of the endosperm described here for *I. crenata*. If, on the other hand, the reference is to the general disintegration of the lateral nucellus, then it represents a distinct variation of the condition in the species treated here. The greatest part of the lateral nucellus, as noted previously, is displaced during the maturation of the megagametophyte.

The Nuclear type of endosperm formation

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of few cells in lower part of raphe; funicular protuberance (P) and tapetum distinct. ×50. FIG. 21. Advanced endosperm; ovule enlarges; lignification slight at apex of integument; hypostase (H) confined to chalaza. ×50. FIG. 22. *Ilex cornuta* Lindl. & Paxt. FIG. 22. Advanced endosperm; ovule enlargement scarcely evident; lignification in integument slight; tapetum less distinct than in other species. ×50. FIG. 23. *Ilex vomitoria* Ait. FIG. 23. Advanced endosperm; lignification confined to micropylar region. ×50. FIG. 24. *Ilex verticillata* (L.) Gray. FIG. 24. Early endosperm development; ovule continues uniform enlargement; differentiation in chalazal epidermis progresses toward micropylar region and may occur in advance of this progression (D). ×75. FIGS. 25–26. *Ilex decidua* Walt. FIG. 25. Early endosperm development; lignification evident in apex of integument, predominantly in region adjacent to funiculus. ×50. FIG. 26. Advanced endosperm; lignification confined to micropylar region. ×50.

occurs in all members of Celastraceae studied by Andersson (1931). Study of endosperm formation in many closely related families indicates that transitional types occur between the Nuclear and Cellular types. In one respect, the endosperm of *Ilex* may be regarded as a transitional type. There frequently is a lapse of time between mitosis and cytokinesis during the early phases of development (Figs. 4 and 5). According to Maheshwari (1950), the total evidence available allows the transition to be read either from the Nuclear toward the Cellular type or vice versa. Endosperm characteristics, therefore, cannot categorically be taken in support of the proposal of a derived status for Celastraceae.

The prominent appearance of lignified cells in the apical region of the integument during endosperm development has been recorded for *I. decidua* and *I. opaca*. Occasional appearance or total absence of lignification in the other species, however, may represent another instance of apparent variation which results directly from infrequent observation. Even in those species which usually disclose extensive lignification at this time, some ovules show complete absence of lignified cells. The cells initially lignified characteristically occur in the region immediately adjacent to the funiculus, and from this area subsequent lignification is extended around the entire circumference of the ovule. Simultaneous appearance of lignified cells around the entire circumference is considered rare.

Summary

The early phases of endosperm development have been studied extensively in *Ilex opaca* Ait. and in somewhat less detail in *I. crenata* Thunbg., *I. cornuta* Lindl. & Paxt., *I. verticillata* (L.) Gray, and *I. decidua* Walt. Suitable fixation of these early phases has not been attained for *I. vomitoria* Ait. In all six species, endosperm development reaches a similar advanced stage prior to the initial division of the zygote.

The pattern of development regarded typical for the genus produces a young endosperm characteristically situated within the anatropous ovule. The primary endosperm is first partitioned to form a secondary endosperm with a chalazal chamber and one or two micropylar chambers in linear sequence. Subsequent divisions produce four cells in each chamber, two toward the side of the ovule on which the micropyle opens, and two on the side toward the raphe. Variations in this pattern of development are recorded and discussed.

Observations reported here are compared with those published by Schürhoff (1921) for *I. aquifolium* L. and with those from related Celastraceae recorded by Andersson (1931).

Structural changes in the ovule associated with endosperm development have been studied in each species. Differentiation of a lignified region in the apex of the integument, a feature characteristic for the genus, shows some variation in the species treated here.

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The Larval Stages of *Panopeus herbstii* Milne-Edwards Reared in the Laboratory[1]

JOHN D. COSTLOW AND C. G. BOOKHOUT
Department of Zoology, Duke University, Durham, N. C., and Duke University Marine Laboratory, Beaufort, N. C.

The larval development of a variety of North American Xanthid crabs has been followed by reconstructing the sequence of larval stages from planktonic material and by rearing the larvae from hatching to the post-larval stages in the laboratory. As early as 1883 Birge described the larval stages of *Neopanope texana sayi* from planktonic material and Conn (1884) briefly discussed the form of the telson of this species before and after hatching. Hyman (1925) described the larval stages of several species from reconstructions at Beaufort, N. C., and Connolly (1925) applied the same technique to *Rhithropanopeus harrisi* from the Miramichi River in Canada. Hart (1935) reared *Lophopanopeus bellus* in the laboratory, and in recent years esveral other species have been reared (*Neopanope texana sayi*, Chamberlain, 1957; *Lophopanopeus leucomanus leucomanus*, Knudsen, 1958).

Although Hyman (1925) describes the prezoea and first zoea of *Panopeus herbstii*, one of the most abundant Xanthids at Beaufort, N. C., the remaining larval stages have not been described either from rearing or from reconstructions. Thus the objectives of this study have been to rear the larvae of *Panopeus herbstii* Milne-Edwards in the laboratory from hatching to the crab stage, and to describe the larval stages which complete the development of this crab.

The authors wish to express their appreciation to Mrs. W. A. Chipman and Mrs. Doris King for their assistance throughout the study. We also thank Dr. Fenner A. Chace for identification of the female from which the larvae were obtained. The adults have been deposited with the U. S. National Museum.

Methods

Ovigerous *Panopeus herbstii* females were placed in finger bowls containing filtered sea water of known salinity which was changed daily. The salinities used (12.5, 20.1, 26.7, and 31.1 p.p.t.) were obtained by diluting sea water of known salinity with distilled water. When hatching occurred the zoeae were removed to separate bowls containing sea water of the same salinity, segregated into groups of 10 zoeae per bowl, and fed *Artemia* nauplii and *Arbacia* eggs. The zoeae were maintained at 20°C., 25°C., and 30°C. with a photoperiod of 12 hours of light and 12 hours of darkness. Approximately 1200 zoeae were maintained in the checked series plus hundreds more in mass cultures of 50 to 75 per finger bowl. The larvae were changed to freshly filtered sea water and clean receptacles daily, the food supply renewed, and the number of molts recorded. Larvae were fixed in Bouin's and 70 per cent alcohol at known intervals during development and exuviae were kept in 70 per cent alcohol to check setation of the appendages.

Drawings were made to scale with the aid of a Whipple disc mounted in the ocular of a compound microscope. The appendages were dissected from each stage larva and drawn to a different scale from that used for the whole larva. Chromatophore patterns for the zoeae and megalops were drawn from living larvae anesthetized with ethyl urathane.

Results

There are four zoeal stages and one megalops stage in the complete larval development of *Panopeus herbstii*. The main morphological characteristics for each larval stage are as follows:

First zoea: The cephalothorax (Fig. 1: A, B) has rostral, lateral, and dorsal spines. The rostral spine is slightly longer than the antennae and the dorsal spine is slightly recurved. The abdomen consists of five segments plus a telson. On segment 2 a short spine projects from the lateral surface, curving slightly anteriorly, and the third abdominal segment bears a smaller

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hook on each lateral surface. The posteriolateral margins of abdominal segments 3 to 5 terminate as long spines which overlap the adjacent segment. A pair of small setae project from the dorsal surface of each abdominal segment. The telson (Fig. 1: A, B) bears a small dorsal spine with two lateral spines, one large and one minute, on the outer surface of each furcus, and three pairs of spines are present on the inner surface of the telson.

Melanophores are distributed in the following pattern: (1) dorsal and median to each eye; (2) posterior and slightly ventral to each eye; (3) dorsal to heart, just posterior to dorsal spine; (4) posteriolateral margins of cephalothorax; (5) mandibles and labrum; (6) first abdominal segment, median and dorsal to gut; (7) abdominal segments 2 to 5, posterioventral surface; (8), basiopodites of maxillipeds 1 and 2. This pattern is modified only by the addition of the sixth abdominal segment, which also has a melanophore on the posteriolateral surface.

The conical antennule (Fig. 1: C) has three large terminal aesthetes and two smaller unequal setae. The protopodite of the antenna (Fig. 1: D) forms a long tapering process with short spines on the distal surface, and the minute exopodite terminates in one short spine. The mandible (Fig. 1: E) has a large ventral tooth and several smaller teeth. The two-segmented endopodite of the maxillule (Fig. 1: F) bears four terminal setae, two subterminal setae, and one seta projecting from the basal segment. The basal endite bears five stout spines and the coxal seven. The unsegmented endopodite of the maxilla (Fig. 1: G) bears three terminal setae, two smaller subterminal setae on one bifurcation, and three terminal setae on the second bifurcation. The endites of the protopodite are also bifurcated, and the basal endite has a total of nine spines while the coxal endite bears eight. The scaphognathite has four soft plumose hairs on the distal margin, and the apical tip is fringed with minute setae. The exopodite of the first maxilliped has four swimming hairs and setation of the five-segmented endopodite is 3, 2, 1, 2, 5 (Fig. 1: H). The three-segmented endopodite of the second maxilliped (Fig. 1: I) has a setation of 1, 1, 5, and the exopodite has four swimming setae (Fig. 1: B).

Second zoea: A slight swelling in the basal portion of the antenna (Fig. 2: D) indicates the beginning of the endopodite. The basal endite of the maxillule (Fig. 2: E) has eight spines and the coxal endite bears a total of seven spines. The maxilla (Fig. 2: F) now has seven hairs on the distal margin of the scaphognathite and three hairs on the apical margin. Six swimming setae project from the exopodite of the first maxilliped (Fig. 2: B) and the second maxilliped (Fig. 2: B) has seven swimming setae.

Third zoea: The developing buds of the third maxilliped and the thoracic appendages extend below the carapace. A sixth abdominal segment is added and small pleopod buds appear on the ventral surfaces of segments 2 to 6 (Fig. 3: A, B). A small pair of spines is added to the inner surface of the telson (Fig. 2: B).

The developing endopodite of the antennule (Fig. 3: C) appears as a small bud and the basal region is slightly swollen. The endopodite bud of the antenna (Fig. 3: D) has increased in size. On the basal endite of the maxillule the spines have increased to nine, and seven spines project from the coxal endite (Fig. 3: E). The basal endite of the maxilla (Fig. 3: F) has ten spines and the coxal endite has eight. A total of eighteen hairs project from the margin of the scaphognathite. The endopodite of the first maxilliped has a setation of 3, 2, 1, 2, 6 (Fig. 3: G), and eight swimming setae are found on the exopodite (Fig. 3, B). A total of nine swimming setae project from the exopodite of the second maxilliped (Fig. 3: A, B).

Fourth zoea: The lateral edges of the carapace (Fig. 4: A) are fringed with short setae and the third maxilliped and thoracic appendages project below the carapace. The antennule is segmented and the three tiers of aesthetes are arranged as 2, 5, 4 (Fig. 4: C). A smaller seta also projects from the terminal segment. The endopodite is present as a small knob. The endopodite of the antenna (Fig. 4: D) is longer and shows slight segmentation. A small unarmed palp appears on the mandible (Fig. 4: E). Setation of the basal and coxal endites of the maxillule has increased to twelve and nine respectively (Fig. 4: F). The basal endite of the maxilla has thirteen spines and nine project from the coxal endite (Fig. 4: G). The exopodite of the first maxilliped has ten swimming setae (Fig. 4: H) and eleven swimming setae are found on the second maxilliped (Fig. 4: I). On the inner surface of the telson a ninth spine, smaller than the others, is added.

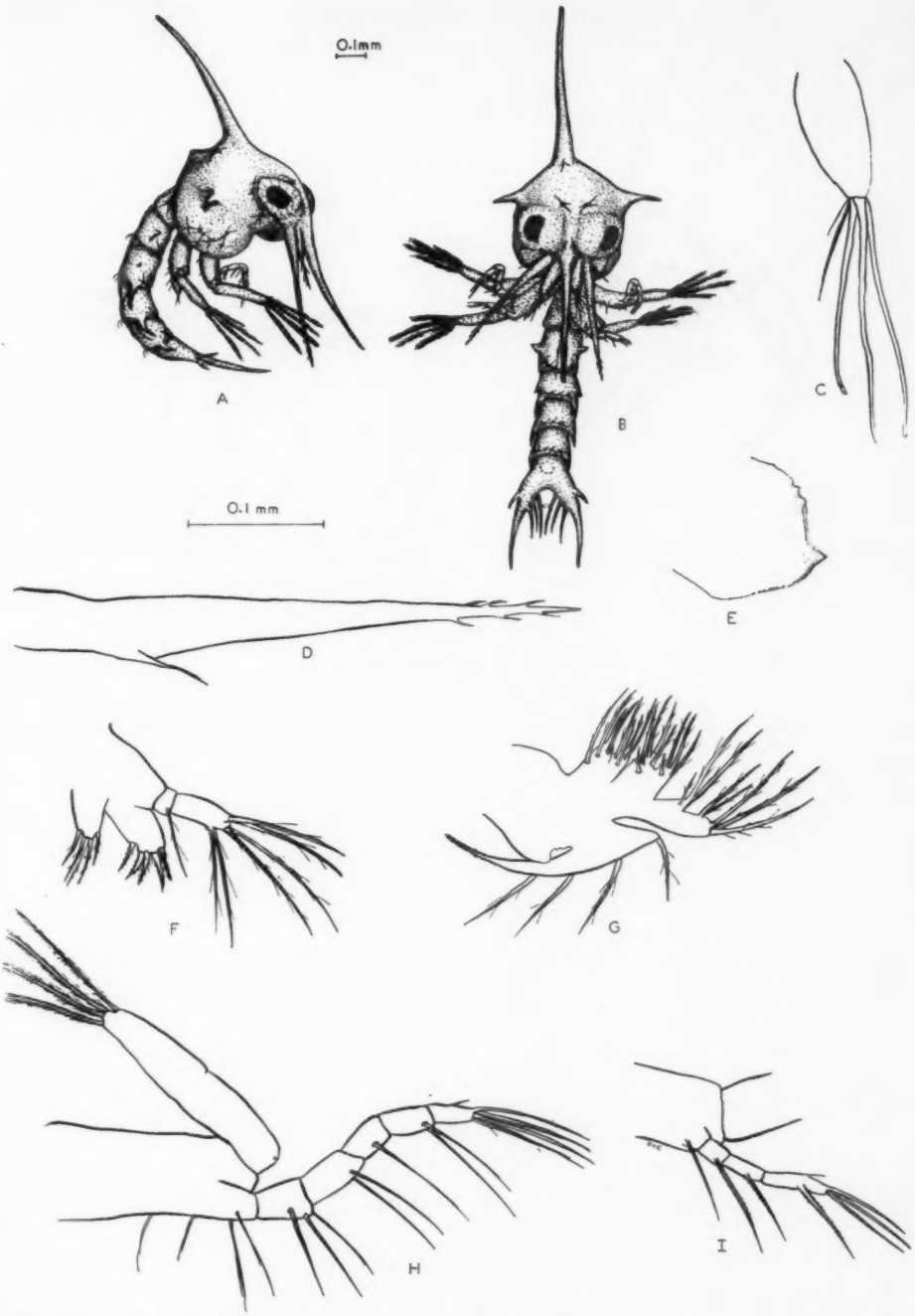

FIG. 1. Side (A) and ventral view (B) of first-stage zoea of *Panopeus herbstii* with appendages. C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, endopodite of second maxilliped.

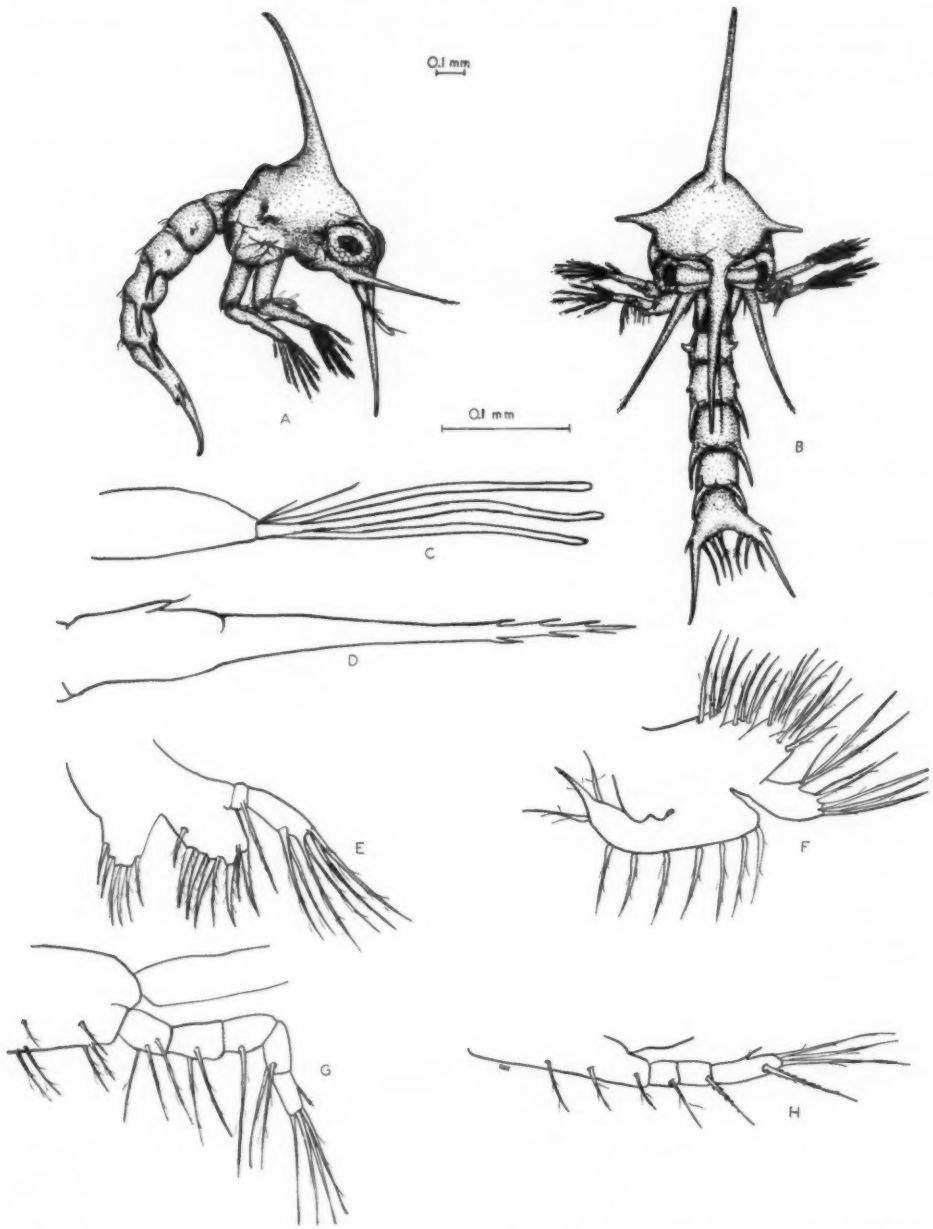

FIG. 2. Side (A) and ventral view (B) of second-stage zoea of *Panopeus herbstii* with appendages. C, antennule; D, antenna; E, maxillule; F, maxilla; G, endopodite of first maxilliped; H, endopodite of second maxilliped.

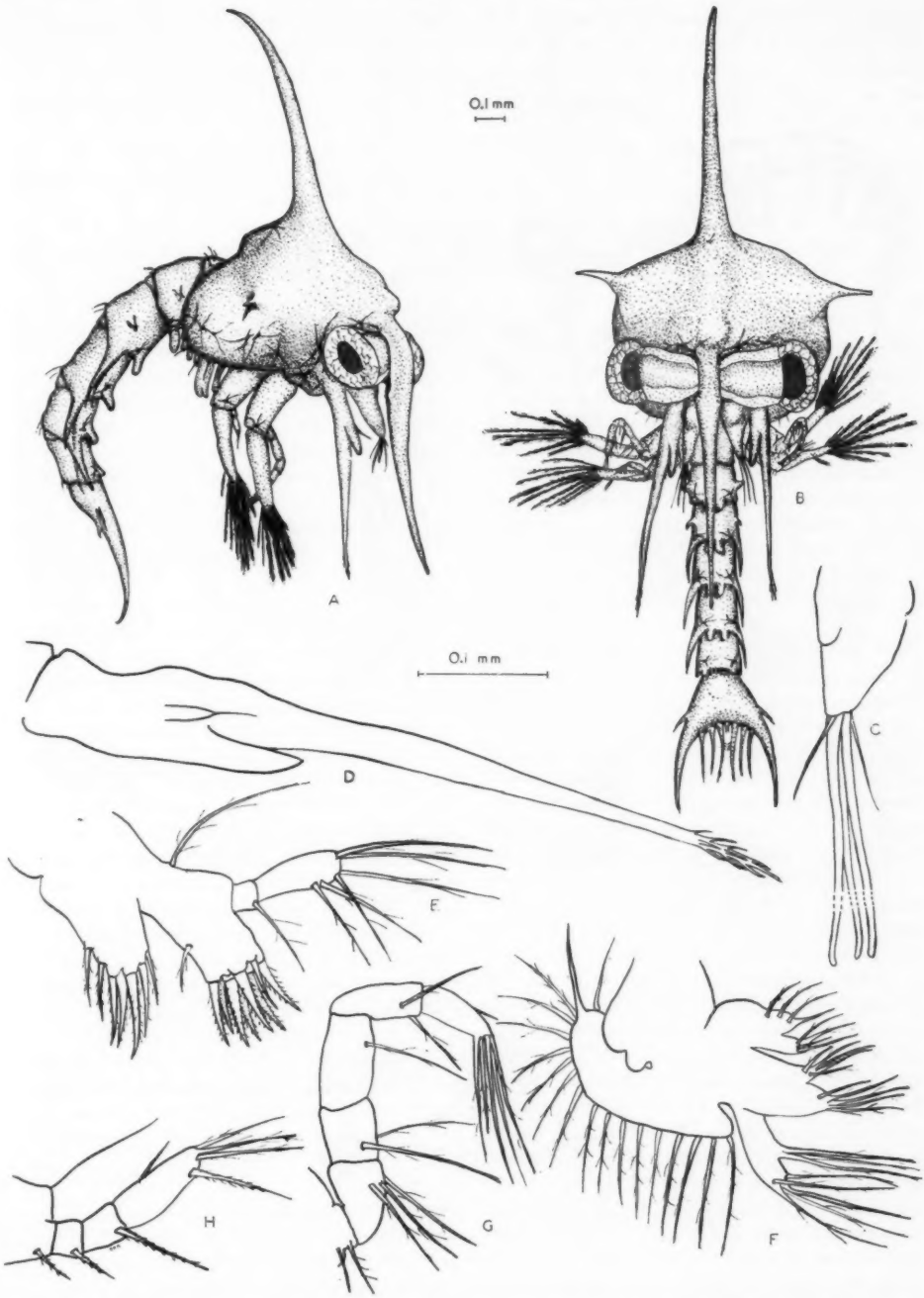

FIG. 3. Side (A) and ventral view (B) of third-stage zoea of *Panopeus herbstii* with appendages. C, antennule; D, antenna; E, maxillule; F, maxilla; G, endopodite of first maxilliped; H, endopodite of second maxilliped.

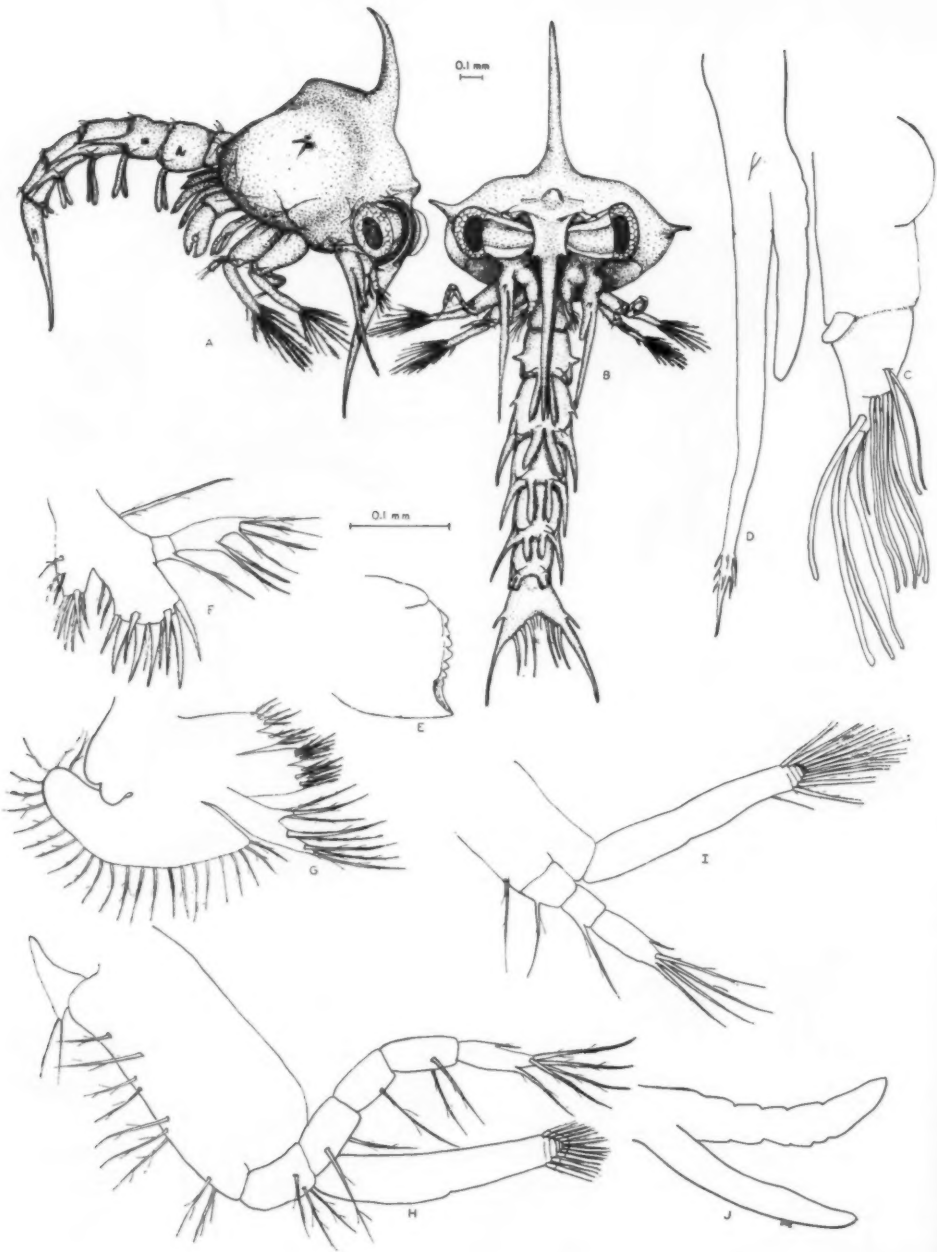

FIG. 4. Side (A) and ventral view (B) of fourth-stage zoea of *Panopeus herbstii* with appendages. C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; second I, maxilliped; J, third maxilliped.

Megalops: The rostrum terminates in a blunt median process which is deflected downward and two stout pointed lateral spines which are slightly shorter than the median process (Fig. 5: A, B). The carapace and thoracic appendages are well provided with short hairs. Of the six abdominal segments, pleopods are present on segments 2 to 6 with a setation of 15, 15, 15, 12, and 8, respectively (Fig. 5: C). Three to six stiff spines project from the caudal margin of the telson. A prominent hook, curving posteriorly, is located on the basi-ishiopodite of the chela (Fig. 5: A). Dactylopodite of the fifth pereiopod has three stiff hairs (Fig. 5: B). The chromatophore pattern of the megalops is as follows: (1) median to the eyes, extending onto the rostrum; (2) posterior to eyes; (3), posteriordorsal surface of carapace; (4) lateral and posterior margins of cephalothorax; (5) basi-ischiopodite of chela and dactylopodite of chela; (6) first abdominal segment, dorsal to gut; (7), posteriolateral borders of abdominal segments 2 to 6.

The antennule (Fig. 5: D) is composed of a peduncle and two flagella. The unsegmented flagellum bears three terminal and two unequal subterminal setae. Aesthetes on the segmented flagellum are arranged in three tiers of eight, six, and four, and the terminal segment has three setae. The antenna has nine segments, some of which bear setae as shown in Figure 5: E. The mandible (Fig. 5: F) bears a two-segmented palp with ten stiff spines on the terminal segment. The maxillule (Fig. 5: G) has four setae on the second segment of the endopodite and three setae on the basal segment. The basal endite has approximately twenty-two spines and the coxal endite has fourteen spines. The endopodite of the maxilla (Fig. 5: H) has three terminal setae and two subterminal groups of two setae each. The bifurcated basal endite bears ten and eight spines on the bifurcations, and the coxal endite has a total of fourteen spines. The scaphognathite is fringed with numerous soft hairs. Setation of the first, second, and third maxillipeds is as shown in Figure 6: A, B, and C.

Discussion

Although the larvae of species of crabs closely related to *Panopeus herbstii* have been described from rearing and planktonic material, only the first zoea of *P. herbstii* has been described and figured (Hyman, 1925). Our description of the first-stage larva differs from that given by Hyman in but a few respects. Hyman (1925) figures a 3:2 setation for the endopodite of the maxillule while we consistently found a 4:2 setation plus one seta on the basal segment (Fig. 1: F). Hyman (1925) also figures a 2:2:3 setation for the endopodite of the maxilla and we found it to be 3:2:3 for all four zoeal stages.

Studies on larvae of other species of Brachyura have shown a progressive increase in the setation of some appendages other than the maxillipeds (Hart, 1935; Costlow and Bookhout, 1959, 1960). There is an increase in setation of both the maxillule and the maxilla in zoeae of *Sesarma cinereum* (Costlow and Bookhout, 1960). In the zoeae of *P. herbstii*, the setation of the basal endite of the maxillule increases with each stage. There is some increase in the setation of the maxilla of *P. herbstii*, but the first and second zoeal stages do not change in this respect. Preliminary studies on the larval development of *Eurypanopeus depressus* reared in the laboratory (Costlow and Bookhout, unpublished results) have shown that the individual zoeal stages of *E. depressus* and *P. herbstii* may be separated by the setation of the coxal and basal endites of the maxillule.

Lebour (1928) notes that within the family Xanthidae the zoeae have three lateral spines on the telson of all stages. She further comments (p. 529), " ... in certain foreign forms, apparently, there may be none at all." Hyman (1925) figures what is apparently a dorsal spine on the telson of larvae from *Neopanope texana sayi* and *Eurypanopeus depressus* and a dorsal and lateral spine on each furcus of the telson of first-stage zoea of *P. herbstii* and *Menippe mercenaria*. We found the dorsal spine plus two lateral spines on each furcus of the telson for all four zoeal stages of *P. herbstii*. Hart (1935) comments that the larval stages of *Lophopanopeus bellus* resemble those of *Rhithropanopeus harrisi* in having only one lateral spine on each form of the telson. Connolly (1925) does not mention spines on the telson of *Rhithropanopeus harrisi* but figures what appears to be only a dorsal spine on each furcus (Connolly, 1925, Figs. 2 and 5). More recently Knudsen (1958) described the telson of *Lophopanopeus leucomanus leucomanus* as having a dorsal spine on each furcus of the telson and noted in the text the absence of lateral spines on the telson. From these descriptions we have two species of the same genus (*Lophopanopeus bellus* and *Lophopanopeus leucomanus leucomanus*) which differ in such general aspects as armature of the telson. Previous studies on larvae of the

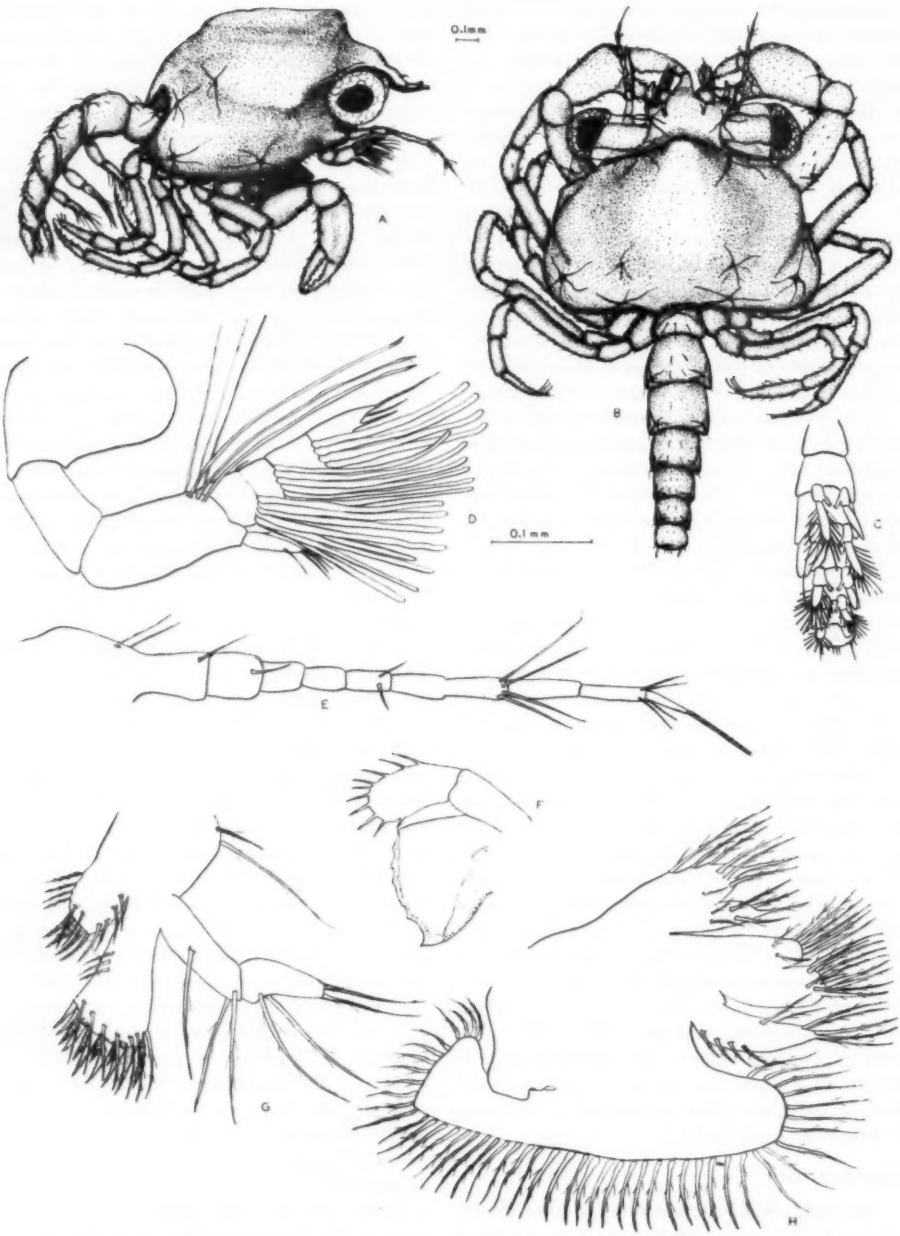

FIG. 5. Side (A) and dorsal view (B) of megalops of *Panopeus herbstii* with appendages. C, ventral view of abdominal segments (setae removed on alternate pleopos for clarity); D, antennule; E, antenna; F, mandible, G, maxillule; H, maxilla.

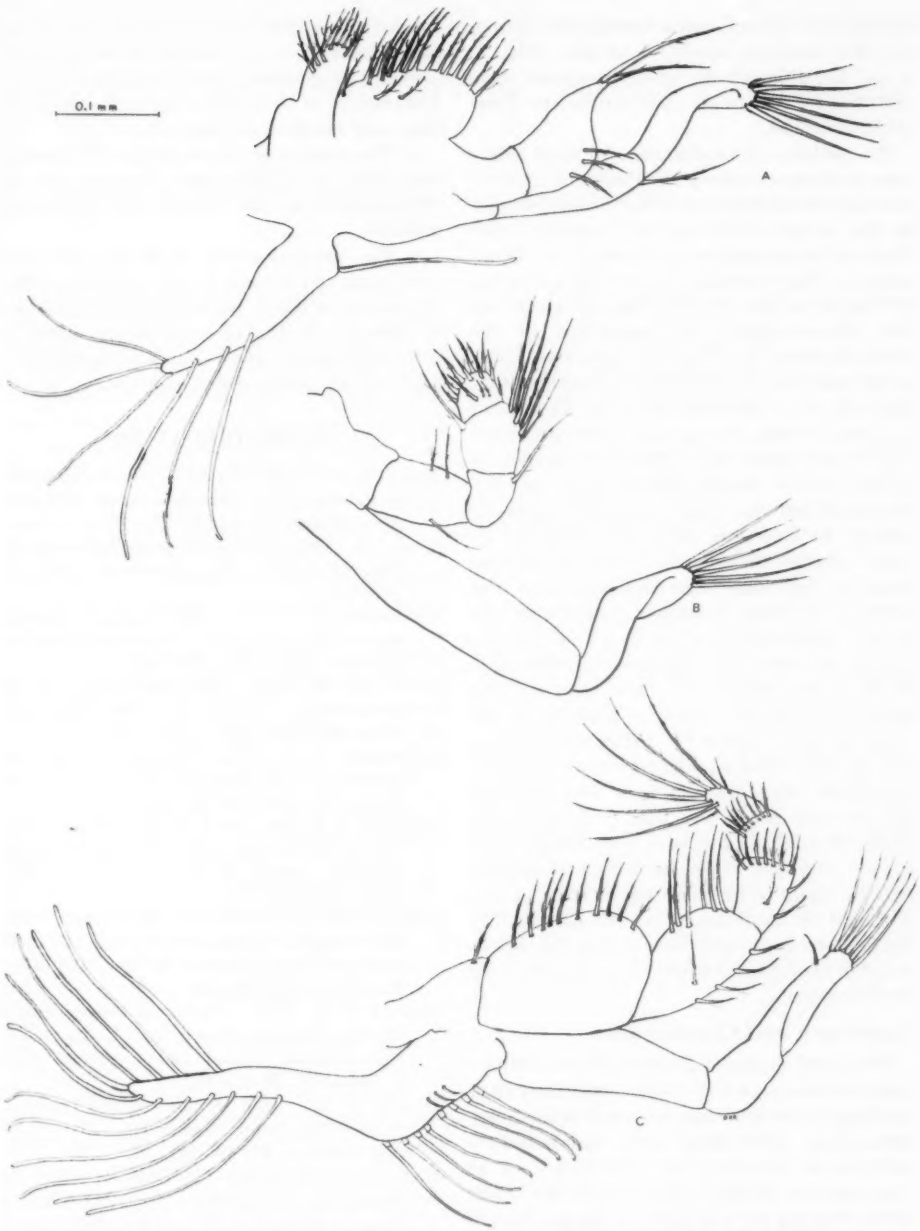

FIG. 6. The maxillipeds of megalops of *Panopeus herbstii*. A, first maxilliped; B, second maxilliped; C, third maxilliped.

Xanthidae, plus the present study, serve to emphasize the variability of spines on the telson of crab larvae from Canada and the Atlantic and Pacific coasts of the United States.

Although previous workers have described several megalops stages for other species of Xanthidae, the present study found only one megalops stage. The megalops stage of *P.*

herbstii has a rostrum which distinguishes it from all other megalops described to date (Fig. 5: A and B), although the second megalops stage described for *Xantho* sp. (unidentified) by Cano (1891) is similar.

The problem of identification of zoeal stages from planktonic material on a basis of setation, size, and chromatophores is made more complex by the nature of the material normally used. Most studies on plankton rely heavily on "fixed" material. While formalin does not affect setation, it is known to alter size to a limited extent, and also chromatophores. A comparison of the chromatophores of living and preserved zoeae of the same species and stage has indicated that there can be considerable difference. In zoeae of *Panopeus herbstii*, for example, chromatophores are not well preserved in Bouin's, formalin, or alcohol. Some chromatophores may be distinguished but the entire pattern is extremely difficult to determine. Prolonged fixation normally increases the difficulty. Even in the living zoeae the individual chromatophores have been observed to change in intensity and the pattern of one individual zoea or megalops may be slightly different from that found in other zoeae of the same species. We have observed that there is a complete range in intensity of the chromatophore pattern for larvae hatched from one egg mass. That is, some larvae are extremely light while others are very dark. This difference may be seen at any one time in larvae reared under identical conditions of food, temperature, salinity, and light. While chromatophore patterns may be useful in identification of larval stages, it should be emphasized that the pattern may not be stable in living larvae and that the pattern found in fixed zoeae can differ from that observed for living forms.

Summary and Conclusion

The larval stages of *Panopeus herbstii* Milne-Edwards have been reared in the laboratory from hatching to the first-stage crab and beyond. Approximately 1200 zoeae were maintained in salinities of 12.5, 20.1, 26.7, and 31.1 p.p.t. at temperatures of 20°C., 25°C., and 30°C. The larvae were fed recently hatched *Artemia* nauplii and fertilized *Arbacia* eggs. From these studies the following conclusions may be made:

1. Under laboratory conditions there are four zoeal stages and one megalops stage. These are described and figured.

2. The setation of all functional appendages has been described and figured for each larval stage. Setation of the endites of the maxillule increases progressively with larval development. The setation of the maxilla increases only in the third and fourth zoeal stages.

3. The rostrum of the megalops of *P. herbstii* may serve as a diagnostic character for the differentiation of this species from planktonic material.

4. The chromatophores of living zoeae and fixed zoeae of *Panopeus herbstii* present a different pattern. Even in the living zoeae the degree of intensity of the chromatophores differs in individuals reared under identical conditions of light, salinity, temperature, and food.

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Synopsis of the Polyporaceae of the Southeastern United States

JOSIAH L. LOWE AND ROBERT L. GILBERTSON
Department of Forest Botany and Pathology, State University College of Forestry at Syracuse University, Syracuse, N. Y.

The Polyporaceae, basidiomycetes with a poroid fruiting surface, are mostly wood-inhabiting organisms with great economic importance. They are among the most important agents causing heartrot of living trees and decay of forest debris and wood in service. The distribution of the species is strongly affected by the available substrate. In the Southeast a tremendous variety of woody plants, along with highly varied climatic conditions, combine to produce a rich flora of polypores. The region has not been explored intensively by mycologists, and it is hoped that this paper will encourage more active field work by the regional collectors.

The Southeast as considered here is arbitrarily delimited on the north by the southern border of Pennsylvania and the Ohio River, and it extends westward to the Great Plains. Within this area woody angiosperms occur in greater variety than in any other area of like size in the North Temperate Zone, and there is a great diversity of gymnosperms as well. The climate is equally variable. A near arctic climate is found at the highest elevations of the Appalachians, and southern Florida and Texas are subtropical; rainfall is favorable practically throughout. No area in temperate North America offers a more rewarding challenge to the mycological collector or systematist.

L. D. deSchweintiz pioneered in mycological work in America by investigating the fungous flora of the Carolinas, and H. W. Ravenel and M. A. Curtis continued collecting in that region. Underwood (1899) summed up the early workers and their contributions, and later publications are cited by Overholts (1953). The most active collectors in the region have been the personnel of the former Division of Forest Pathology and the present Division of Forest Disease Research, Forest Service, U.S.D.A., but mycologists associated with educational institutions have also been important contributors, particularly W. C. Coker of the University of North Carolina and L. R. Hesler of the University of Tennessee. Lloyd (1899–1925), Murrill (1907–08), and Overholts (1953) have rendered the valuable service of collecting scattered records and publishing manuals.

This synopsis is a preliminary paper presenting taxonomic information now available. Distributional data for the pileate species is based on the Overholts' manual (1953); for the genus *Poria*, on Overholts' manuscript records and on Baxter's papers (1932–1955). These records are supplemented by data from approximately 2500 collections from the Southeast made by Lowe in 1950, and 1951 and by Lowe and Gilbertson in 1959, and by new records from the study of herbarium specimens, principally at the National Fungus Collections and the New York Botanical Garden. Types or authentic specimens have been examined for all species except those enclosed in brackets. Most species are restricted to a woody substratum and this is to be understood where the substratum is stated. The classification adopted is the conservative treatment of Overholts (1953), partly because it is practically useful, partly because more exact morphological data is needed to employ a different scheme. The microscopic details are based on examination of thin sections of material mounted in 2 per cent potassium hydroxide (KOH) solution.

In this paper 293 species and 7 varieties are considered valid elements of the flora. *Poria eyrei* and *P. latitans* are reported for the first time from North America. *Poria salmonicolor*, widely cited as a synonym of *P. spissa*, is considered a valid species which antedates *P. rubens*.

KEY TO THE GENERA

1a. Spores brown, ellipsoid, truncate at one end, appearing echinulate V. GANODERMA

1b. Spores colored to hyaline, smooth, or if echinulate, then not truncate

2a. Sporophores always resupinate IV. PORIA

2b. Sporophores stipitate, sessile, or effused-reflexed, sometimes resupinate at first
3a. Sporophores perennial, with tubes in more or less distinct layers II. FOMES
3b. Sporophores annual, with one layer of tubes, occasionally reviving a second year
4a. Hymenophore typically labyrinthine VI. DAEDALEA
4b. Hymenophore typically radially lamellate VII. LENZITES
4c. Hymenophore poroid, the pores circular to angular, or rarely concentrically lamellate
5a. Pores distinctly hexagonal or diamond shaped, radially elongated; sporophores laterally stipitate, light colored VIII. FAVOLUS
5b. Pores hexagonal; pileus sessile, dark IX. HEXAGONA
5c. Pores circular to angular, rarely radially elongated
6a. Trama and context often different in texture; sporophore texture and spore shape very variable I. POLYPORUS
6b. Trama continuous with the context tissue; spores always cylindric III. TRAMETES

I. *POLYPORUS* Mich. ex Fries

1a. Context white or bright colored
2a. Sporophore stipitate
3a. Spores broadly ellipsoid to globose
4a. Spores spiny-tuberculate or pitted

1. POLYPORUS BERKELEYI Fries. Spores echinulate, globose to subglobose, 7–8 × 6–7 μ. On living angiosperms throughout except Del., Miss., Okla., and Kans. Syn.: *beatiei* Bann., *lactifluus* Peck, *?subabortivus* (Murr.).
2. POLYPORUS GRISEUS Peck. Spores tuberculate, 5–6 × 3.5–5 μ. On the ground in Va., N. C., Ga., Ala., and Tenn. Syn.: *carlei* Underw.
3. POLYPORUS SUBLIVIDUS (Snell) Lowe. Spores pitted, ovoid to subglobose, 8–12 × 8–10 μ. On ground in N. C. and Tenn. Syn.: *canaliculatus* Overh.

4b. Spores smooth
5a. Spores conspicuously apiculate, more or less tear-shaped

4. POLYPORUS ELLISII Berk. Pileus greenish yellow and conspicuously scaly. On the ground in N. C., Ala., and Ky. Syn.: *flavo-squamosus* Underw.
5. POLYPORUS PES-CAPRAE Pers. ex Fries. Pileus reddish brown, scaly. On the ground in N. C., Ga., Ala., and Tenn. Syn.: *retipes* Underw.

5b. Spores ovoid to ellipsoid, apiculus inconspicuous
6a. Sporophores fleshy, drying cheesy to rigid
7a. Spores 3–6 μ wide

6. POLYPORUS CRISTATUS Pers. ex Fries. Pileus yellowish or greenish when fresh. On the ground in Del., Md., D. C., W. Va., Va., N. C., S. C., Fla., Ala., Tenn., Mo., and Ark. Syn.: *?cristatiformis* (Murr.), *flavovirens* Berk. & Rav.
7. POLYPORUS PERSICINUS Berk. & Curt. Pileus buff to pinkish brown when fresh; drying very light in weight. On the ground in N. C., S. C., Fla., and Ark.
8. POLYPORUS CAERULEOPORUS Peck. Pileus grayish to pale blue when fresh, drying brownish or reddish. On the ground in N. C. Syn.: *holocyaneus* Atk.
9. POLYPORUS STEWARTAE Coker. Pileus reddish buff. On ground in N. C.

7b. Spores 2–3 μ wide

10. POLYPORUS OVINUS Schaeff. ex Fries. White, in age darkening, on drying reddish or olivaceous. On the ground under gymnosperms in Tenn.
11. POLYPORUS CONFLUENS Alb. & Schw. ex Fries. Yellowish or ochre to reddish when fresh, drying reddish. On the ground in W. Va., N. C., S. C., Ala., Ky., and Tenn. Syn.: *laeticolor* (Murr.), *?subrufescens* Murr.
12. POLYPORUS PECKIANUS Cooke. Yellow or buff, drying pale tan; context white. On the ground or on buried wood of angiosperms in Tenn.

6b. Sporophores tough or fibrous when fresh
8a. Spores 5–9 μ long
9a. Sporophore simple, pileus usually solitary on stipe

13. POLYPORUS BIENNIS (Bull. ex Fries) Fries. Cystidia abundant; pores 1–3 per mm.; globose chlamydospores in context. On the ground under angiosperms in Del., Md., D. C., N. C., Ga., Fla., Ala., Tenn., Ky., Mo., Ark., La., and Texas. Syn.: *abortivus* Peck, *distortus* (Schw.), *?tisdalei* (Murr.).
14. POLYPORUS DEALBATUS Berk. & Curt. Cys-

tidia lacking; pileus distinctly zonate above; pores 6–7 per mm. On the ground in N. C., S. C., and Fla.

9b. Sporophore compound, pilei many on a much-branched stipe

15. POLYPORUS GIGANTEUS Pers. ex Fries. Individual pilei up to 15 cm. broad; pores 4–7 per mm. On the ground under angiosperms in Md., D. C., W. Va., Va., N. C., Ala., Tenn., Mo., and La.

16. POLYPORUS FRONDOSUS Dicks. ex Fries. Individual pilei up to 7 cm. broad; pores 2–4 per mm. On the ground at the base of living and dead angiosperms in Md., D. C., W. Va., N. C., Ga., Tenn., Mo., Ark., and La.

8b. Spores 3–5.5 μ long

17. POLYPORUS FRACTIPES Berk. & Curt. Context duplex; pores 4–5 per mm. On angiosperms in S. C., Tenn., and Mo.

18. POLYPORUS MUTABILIS Berk. & Curt. Pileus distinctly zonate above; pores 6–8 per mm. On angiosperms, rarely gymnosperms, in Del., Ga., Fla., Ala., Tenn., Ky., Mo., Ark., and La.

19. POLYPORUS FIMBRIATUS Fries. Sporophore branched into many pilei; margin of pileus usually fimbriate; pores radially elongate, 2–3 per mm. On angiosperms in Ala. and La.

3b. Spores cylindrical to narrowly ellipsoid or subfusiform

10a. Spores 4–8 μ wide, 10 μ or more long

20. POLYPORUS SQUAMOSUS Mich. ex Fries. Sporophores laterally stipitate; upper surface scaly; stipe black at base. On angiosperms in Md., W. Va., N. C., Tenn., Ky., Mo., Ark., and Kans.

21. POLYPORUS RADICATUS Schw. Sporophores centrally stipitate; upper surface fibrillose to scaly; stipe with a long, black, rootlike base. On the ground under angiosperms in Md., Ala., Tenn., Mo., and Kans. Syn.: *kansensis* Ell. & Barth.

10b. Spores 2.5–4 μ wide, usually less than 10 μ long

11a. Stipe black at the base

22. POLYPORUS PICIPES Fries. Pilei up to 20 cm. broad; upper surface reddish brown to dark brown. On angiosperms in D. C., Md., W. Va., N. C., Ala., Tenn., Ky., Mo., Ark., and Kans.

23. POLYPORUS VARIUS Fries. Pilei up to 12 cm. broad; upper surface usually tan with lighter radial striations. On angiosperms in D. C., W. Va., N. C., Tenn., and Mo.

24. POLYPORUS ELEGANS Bull. ex Fries. Pilei up to 7 cm. broad; upper surface pale tan, weathering to white. On angiosperms, rarely on gymnosperms, in Del., W. Va., Va., N. C., Ala., Tenn., Ky., and Ark.

25. POLYPORUS BLANCHETIANUS Berk. & Mont. Pilei up to 5 cm. broad; upper surface tan to bright chestnut brown or blackish. On angiosperms in Fla.

26. POLYPORUS VIRGATUS Berk. & Curt. With branched hairs on the upper surface. A species of uncertain identity, a single collection reported on angiosperms in Fla.

11b. Stipe not black at the base

12a. Pores more or less diamond shaped, usually radially elongated

27. POLYPORUS ARCULARIUS Batsch ex Fries. Upper surface squamulose; margin often ciliate; spores 7–11 μ long. On angiosperms throughout except Ark. Syn.: *arculariformis* Murr.

28. POLYPORUS BRUMALIS Pers. ex Fries. Upper surface densely hispid to scabrous; spores 5–7 μ long. On angiosperms in Del., D. C., W. Va., Tenn., Ky., Ark., and Kans.

12b. Pores circular to angular

13a. Stipe centrally attached; sporophores developing on the ground

29. POLYPORUS UMBELLATUS Pers. ex Fries. Pilei many on a much-branched stipe. On the ground in Tenn., Ky., and Kans.

30. POLYPORUS CRYPTOPUS Ell. & Barth. Pileus solitary on stipe. On dead grass roots in Kans.

13b. Stipe laterally or dorsally attached; sporophores developing on wood

31. POLYPORUS FLORIFORMIS Quél. Sporophores laterally substipitate or in a rosette, often petal-like; bitter. On gymnosperms and angiosperms in N. C. and Tenn.

32. POLYPORUS POCULA (Schw.) Berk. & Curt. Sporophores pendent, up to 5 mm. broad. On angiosperms in Del., W. Va., Va., N. C., S. C., Ga., Fla., Ala., Tenn., and Mo. Syn.: *cupulaeformis* Berk. & Curt., *pendulus* (Schw.).

33. POLYPORUS BETULINUS Bull. ex Fries. Sporophores laterally substipitate, up to 25 cm. broad and 10 cm. thick; upper surface whitish

to tan with a distinct pellicle. On Betula in W. Va., N. C., Tenn., and Kans.

2b. Pilei sessile or effused-reflexed

14a. Volva present

34. POLYPORUS VOLVATUS Peck. On recently killed gymnosperms in Del., Md., D. C., W. Va., Va., and Fla.

14b. Volva absent, tubes exposed from the first

15a. Context distinctly colored orange or red

35. POLYPORUS CINNABARINUS Jacq. ex Fries. Red or yellowish red; upper surface of pileus somewhat tomentose; pileus 5–20 mm. thick. On angiosperms or rarely on gymnosperms throughout except Fla. and Texas.

36. POLYPORUS SANGUINEUS L. ex Fries. As in *P. cinnabarinus* except upper surface much smoother, as if seared, and pileus 2–5 mm. thick. On angiosperms throughout.

37. POLYPORUS FIBRILLOSUS Karst. Orange; pores 1.5–2 per mm.; cystidia present. On gymnosperms or rarely on angiosperms in W. Va.

38. POLYPORUS CROCEUS Pers. ex Fries. Orange; pores 2–4 per mm.; sporophore blackening and resinous on drying. On angiosperms, especially chestnut, in Del., W. Va., Va., N. C., S. C., Fla., Tenn., Ky., Mo., and Ark. Syn.: *castanophilus* Atk., *pilotae* Schw.

15b. Context white to cream or pale yellow

16a. Spores cylindrical to ellipsoid

17a. Pileus usually rather soft and watery when fresh, drying rigid or rarely soft

18a. Context bitter

39. POLYPORUS GUTTULATUS Peck. Pileus typically applanate, the surface spotted above; spores 2–2.5 μ wide. On gymnosperms or rarely on angiosperms in Va., N. C., Tenn., and Ky.

40. POLYPORUS IMMITIS Peck. Pileus convex, the surface typically rough with scattered nodules when dry; spores 1.5–2 μ wide. On gymnosperms and angiosperms in Tenn.

41. POLYPORUS TEPHROLEUCUS Fries. Pileus convex, the surface usually drying pelliculose; spores 0.7–1 μ wide. On angiosperms or rarely gymnosperms in Del., Md., D. C., W. Va., N. C., Tenn., Mo., and Kans. Application of the specific name is in the sense of Overholts, doubtfully valid, as mycologists of northern Europe apply this name to a gray form of a sporophore similar to *P. albellus*.

18b. Context mild

19a. Tissue pale purplish red, turning red on bruising or drying, or red from the first

42. POLYPORUS MOLLIS Pers. ex Fries. Context hyphae septate. On gymnosperms in Fla., Ala., Ark., La., and Texas. Syn.: *smallii* (Murr.).

43. POLYPORUS FRAGILIS Fries. Context hyphae clamped. On gymnosperms in D. C., Va., N. C., ?Fla., and Tenn. Syn.: *?leucomallellus* (Murr.), *?newellianus* Murr.

19b. Tissue unchanged on bruising or drying, or somewhat bluish

44. POLYPORUS CAESIUS Schrad. ex Fries. Pores 2–4 per mm.; often distinctly pubescent above; often with some blue coloration. On angiosperms and gymnosperms in Del., D. C., W. Va., Va., N. C., Ala., Tenn., Ky., and Mo.

45. POLYPORUS ALBELLUS Peck. Pores 3–5 per mm., glabrous or nearly so and often pelliculose above. On angiosperms or rarely on gymnosperms in Md., Va., N. C., Fla., Tenn., and Ky.

46. POLYPORUS SEMIPILEATUS Peck. Pores 5–8 per mm. On angiosperms in Del., D. C., Va., N. C., Ga., Fla., Ala., Tenn., Ky., Mo., and La.

17b. Pileus coriaceous, or tough when fresh and corky when dry

20a. Trama and subhymenial tissue of different color or consistency from the context

21a. Pore surface white, pink, purplish, red, or orange; trama and subhymenial tissue more or less gelatinized

47. POLYPORUS SUBCARTILAGINEUS Overh. Pore surface white when fresh, brownish or reddish on drying; spores 2–3 μ wide. On gymnosperms in Tenn.

48. POLYPORUS AMORPHUS Fries. Pore surface usually pink to red or orange; spores 0.7–1 μ wide; pores 2–4 per mm. On gymnosperms in Md., D. C., Va., N. C., Miss., Tenn., and Ark. Syn.: *pini-glabrae* (Murr.).

49. POLYPORUS DICHROUS Fries. Pore surface usually distinctly reddish purple; spores 0.5–1 μ wide; pores 5–8 per mm. On angiosperms or rarely on gymnosperms throughout except Miss. and Texas.

21b. Pore surface dark brown to blackish; trama and subhymenial tissue fibrous

50. POLYPORUS ADUSTUS Willd. ex Fries. Without odor when fresh; dark line at base of tubes usually distinct; trama dark in KOH. On angiosperms, rarely gymnosperms, throughout. Intergrades with the next. Syn.: *alabamensis* (Murr.).

51. POLYPORUS FUMOSUS Pers. ex Fries. Fragrant when fresh; dark line indistinct or absent; trama hyaline or nearly so in KOH. On angiosperms in Del., Md., D. C., W. Va., Fla., Tenn., Ky., Mo., Ark., La., Texas, and Kans.

20b. Trama and subhymenial tissue of about the same color and consistency as the context

22a. Context usually 5 mm. or more thick

23a. Tissue distinctly darkening in KOH solution

52. POLYPORUS RESINOSUS Schrad. ex Fries. Dark brown to blackish brown above; spores 4–7 μ long. On angiosperms and gymnosperms in Md., D. C., W. Va., Va., N. C., Fla., Tenn., Ky., Mo., Ark., and Kans.

53. POLYPORUS SUPINUS Swartz ex Fries. White to tan above and becoming red or blackish toward base; spores 9–10 μ long. On angiosperms in N. C., S. C., Ga., Fla., Ala., Miss., Ark., La., and Texas.

23b. Tissue unchanged in KOH solution

24a. Tissue resinously disagreeable in taste

54. POLYPORUS ANCEPS Peck. Context hyphae dendritically branched, tapering to whiplike extremities. On gymnosperms in Md., Va., Miss., and La.

55. POLYPORUS PALUSTRIS Berk. & Curt. Context hyphae uniform in diameter; context slightly fibrous. On gymnosperms in S. C., Ga., Fla., Miss., Ark., and La.

56. POLYPORUS DURESCENS Overh. As above except on angiosperms in D. C., Va., Ga., Miss., Tenn., Ky., and La.

24b. Tissue mild in taste

57. POLYPORUS MELIAE Underw. Without taste; context distinctly fibrous. On angiosperms in N. C., Fla., Ala., Tenn., Mo., Ark., La., and Texas. Syn.: *submurinus* (Murr.).

22b. Context usually much less than 5 mm. thick

25a. Cystidia present

26a. Pores 1–2 per mm.

58. POLYPORUS VERSATILIS (Berk.) Rom. Pore surface and often entire sporophore some shade of brown; cystidia small, usually capitate incrusted. On gymnosperms and angiosperms in N. C., Fla., Ala., La., and Texas.

59. POLYPORUS TULIPIFERAE (Schw.) Overh. Sporophore white; cystidia large, incrusted. On angiosperms or rarely on gymnosperms throughout except Miss., Texas, and Okla.

26b. Pores 2–4 or more per mm.

27a. Pileus strigose to pubescent above

60. POLYPORUS ABIETINUS Dicks. ex Fries. Context with a definite cuticular layer. On gymnosperms throughout except Okla. and Kans.

61. POLYPORUS PARGAMENUS Fries. Context homogeneous, white. On angiosperms throughout except Okla. and Kans.

62. POLYPORUS SECTOR Ehrenb. ex Fries. As above except darker throughout and restricted to the coastal states—N. C., S. C., Ga., Fla., Ala., La., and Texas.

27b. Pileus with fibrils or hydnoid processes above

63. POLYPORUS TRICHOMALLUS Berk. & Mont. Sporophore brown to blackish. On angiosperms in Fla. This species might be sought in the brown section of Polyporus; compare with No. 111.

27c. Pileus appressed-fibrillose above

64. POLYPORUS BALSAMEUS Peck. On gymnosperms or rarely on angiosperms in N. C. and Tenn.

25b. Cystidia lacking

28a. Pores 1–5 per mm.

29a. Upper surface conspicuously hirsute to villose

65. POLYPORUS PINSITUS Fries. Pores 1–3 per mm.; spores 5–8 × 2.5–3.5 μ. On gymnosperms or rarely on angiosperms in Va., N. C., S. C., Ga., Fla., Ala., Tenn., Ky., Mo., Ark., La., Texas, and Okla.

66. POLYPORUS VERSICOLOR L. ex Fries. Pores 3–5 per mm.; pileus with multicolored zones

and silky-villose or velvety above; spores 4–6 × 1.5–2 μ. On angiosperms or rarely on gymnosperms throughout.

67. POLYPORUS MAXIMUS (Mont.) Overh. Pores 3 per mm.; spores 4–5 × 2–2.5 μ; context 1–5 mm. thick, with a distinct line separating tomentum from context. On angiosperms in Fla. and La.

68. POLYPORUS HIRSUTUS Wulf. ex Fries. Pores 3–4 per mm.; unicolorous and hirsute or tomentose above; context without a line; spores 4.5–7 × 2–2.5 μ. On angiosperms throughout except Del. and Okla.

29b. Upper surface inconspicuously tomentose to glabrous

30a. Sterile cup usually present at base of pileus

69. POLYPORUS CONCHIFER (Schw.) Fries. On angiosperms, usually elm, in Del., Md., W. Va., Va., Ga., Ala., Tenn., Ky., Mo., Ark., La., and Kans.

30b. Sterile cup never present

70. POLYPORUS BIFORMIS Fries. Pores 1–2 per mm.; pileus drying rough-fibrillose above; spores 6–8 × 2–2.5 μ. On angiosperms or rarely on gymnosperms throughout except S. C., Miss., and Ky.

71. POLYPORUS UNDOSUS Peck. Pores 1–2 per mm.; pileus drying compactly villose above; spores 4–6 × 1–1.5 μ. On gymnosperms or rarely on angiosperms in W. Va., Va., N. C., and Tenn.

72. POLYPORUS PUBESCENS Schum. ex Fries. Pores 3–4 per mm.; upper surface uniform; spores 5–8 μ long. On angiosperms in W. Va., N. C., Tenn., and Kans.

73. POLYPORUS CERIFLUUS Berk. & Curt. Pores 3–4 per mm.; upper surface more or less reddish and spotted; spores 4–5 μ long. On angiosperms in S. C., known only from the type.

28b. Pores usually 5 or more per mm.

31a. Context corky to subfibrous when dry

74. POLYPORUS MODESTUS Kunze. Pore surface and context more or less pink; context hyphae thin walled; spores unknown. On angiosperms in Fla.

75. POLYPORUS ECTYPUS Berk. & Curt. Context white; spores straight or slightly curved, 2–3 μ wide; pileus becoming red at base. On angiosperms in N. C., S. C., Ga., Fla., Mo., and La.

76. POLYPORUS SUBECTYPUS (Murr.) Bres. Context white; spores straight, 1–2 μ wide; white to tan above. On angiosperms in Ga., Fla., and La.

77. POLYPORUS OCHROTINCTELLUS (Murr.) Overh. Context white; spores distinctly allantoid; sporophore often narrowed at base and substipitate. On angiosperms in Fla. and Miss.

31b. Context distinctly fibrous

78. POLYPORUS TENUIS (Sacc.) Overh. Glabrous or nearly so above, whitish to yellowish. On cypress in S. C., Ga., Fla., Mo., and La. Differs from the next only in its paler color.

79. POLYPORUS DRUMMONDII Klotzsch. As above but more or less distinctly brown; spores unknown. On cypress in Fla. and La.

16b. Spores ellipsoid to ovoid or globose

32a. Context hyphae septate; pores 6–9 per mm. (see also No. 94).

80. POLYPORUS RIGIDUS Lév. Subresupinate; drying rough and more or less tomentose above. On angiosperms in Md., W. Va., Fla., Ala., Mo., and La.

81. POLYPORUS ZONALIS Berk. Usually sessile; drying minutely pubescent to glabrous above. On angiosperms in Fla., Ala., Miss., and La. Delimitation of this and the preceding species is not yet satisfactory.

32b. Context hyphae with clamps or appearing nonseptate; pores 1–7 per mm.

33a. Spores 2.5–5 μ long

34a. Pores 1–4 per mm.

82. POLYPORUS ACULEIFER (Berk. & Curt.) Overh. Pileus with fibrils or hydnoid processes above. On angiosperms in Fla.

83. POLYPORUS AMYGDALINUS Berk. & Rav. Tomentose-velutinous above; very light in weight when dry; pores 3–4 per mm. On angiosperms in S. C., Fla., Ala., and La.

84. POLYPORUS FISSILIS Berk. & Curt. Tomentose or fibrillose above; heavy and hard when dry; pores 1–3 per mm. On angiosperms in Md., W. Va., Va., N. C., Ga., Fla., Ala., Tenn., Ky., and La. Syn.: *?humeanus* (Murr.); *?tigertianus* (Murr.).

34b. Pores 4–7 per mm.

35a. Pileus soft and watery when fresh

85. POLYPORUS FUMIDICEPS (Atk.) Sacc. & Trott.

Gray to brown above; tubes usually greenish on drying. On angiosperms in Del., Md., Tenn., and Mo. Syn.: ?*pseudolacteus* Murr.

86. POLYPORUS GALACTINUS Berk. White or whitish above; tubes drying white or yellowish. On angiosperms in Del., Md., D. C., W. Va., Va., N. C., Ala., Tenn., Ky., Mo., Ark., and La.

35b. Pileus corky or cartilaginous-tough when fresh

87. POLYPORUS CALKINSII (Murr.) Sacc. & Trott. Corky when fresh; pileus convex to subungulate, 10–40 mm. thick; spores globose. On angiosperms in Fla.

88. POLYPORUS SEMISUPINUS Berk. & Curt. Cartilaginous-tough when fresh; pileus 1–3 mm. thick; spores ellipsoid. On angiosperms or rarely on gymnosperms in Va. and Tenn.

33b. Spores 4.5–10 μ long

36a. Pores 1–3 (rarely 4) per mm.

37a. Cystidiate; on gymnosperms

89. POLYPORUS BOREALIS Fries. In Va., N. C., and Tenn.

37b. Noncystidiate; on angiosperms

90. POLYPORUS OBTUSUS Berk. Hirsute-tomentose above; pores 1 or less per mm.; pileus convex to ungulate. On angiosperms in Md., D. C., Va., N. C., Ga., Fla., Ala., Miss., Tenn., Mo., Ark., La., Okla., and Kans.

91. POLYPORUS SPUMEUS Sow. ex Fries. Villose-strigose or strigose-tomentose above; pores 2–4 per mm. On angiosperms in W. Va., Tenn., and Mo. Var. *malicola* Lloyd is a thin form with spores 4–5 × 3.5–4 μ; reported from Tenn.

92. POLYPORUS DELECTANS Peck. Finely tomentose to glabrous above; pores 1–2 per mm. On angiosperms in Del., Md., D. C., Va., Tenn., and Mo.

36b. Pores 3–6 or more per mm.

38a. Chlamydospores present in context

93. POLYPORUS COMPACTUS Overh. Sporophore nodular; pores 3–4 per mm.; clamps present on smaller context hyphae; chlamydospores 8–11 × 7–9 μ. On angiosperms in Md. and Tenn.

94. POLYPORUS ROBINIOPHILUS (Murr.) Lloyd. Sessile, often imbricate; pores 4–6 per mm.; context hyphae inconspicuously septate; chlamydospores 5–7 × 3–5 μ. On angiosperms in Md., D. C., W. Va., Va., Ga., Fla., Miss., Tenn., Ky., Mo., Texas, and Kans. Syn.: ?*magnisporus* Murr.

38b. Chlamydospores absent from context

95. POLYPORUS SPRAGUEI Berk. & Curt. Pileus 6–30 mm. thick, corky to rigid, appressed-tomentose to usually glabrous above; sporophore often blackening when dry. On angiosperms in D. C., W. Va., Va., N. C., Ga., Tenn., Mo., Ark., and La.

96. POLYPORUS PAVONIUS (Hook.) Fries. Pileus coriaceous, 1–2 mm. thick; villose or tomentose above. On angiosperms in Fla. and La.

1b. Context brown

39a. Sporophores stipitate

40a. Spores more or less brown

41a. Pores 2–4 per mm.

42a. Sporophores erect

97. POLYPORUS CINNAMOMEUS Jacq. ex Fries. Upper surface silky-fibrillose, shining. On the ground in Del., Md., D. C., W. Va., Va., N. C., Ga., Ala., Miss., Tenn., Ky., Mo., and La.

98. POLYPORUS PERENNIS L. ex Fries. Upper surface tomentose to glabrous, dull. On the ground in Md., Va., N. C., Ga., Fla., Ala., Tenn., and Mo.

99. POLYPORUS MOWRYANUS Murr. Sporophores on wood; upper surface shining, usually radially fibrillose; scattered setae present. On angiosperms in Fla.

42b. Sporophores pendent on a short dorsal stipe

100. POLYPORUS DEPENDENS Berk. & Curt. Spores minutely roughened, 8–10 × 4–5 μ. On angiosperms in Va., N. C., S. C., Fla., and Tenn.

41b. Pores 0.5–2 mm. in diameter or hymenophore concentrically lamellate

101. POLYPORUS FOCICOLA Berk. & Curt. Spores 7–11 × 4–4.5 μ; context hyphae 4–7 μ in diameter. On the ground in Del., N. C., and S. C.

102. POLYPORUS MONTAGNEI Fries. Spores 8–12 × 4.5–6 μ; context hyphae mostly 9–12 μ in diam. On the ground in Del., Md., D. C., W. Va., N. C., Tenn., and Ky. Var. *greenei* (Berk.) Gilberts. has the hymenophore in the form of concentric lamellae. Syn.: *obesus* (Ell. & Everh.), *memmingeri* (Murr.).

40b. Spores hyaline

43a. Setae present

103. POLYPORUS TOMENTOSUS Fries. Context duplex; context hyphae 3–7 μ in diam.; pore

surface light to dark yellowish brown. On the ground under gymnosperms in Del., Md., D. C., W. Va., N. C., S. C., Ala., and Tenn. Var. *circinatus* (Fries) Sartory & Maire has thicker sessile sporophores that develop on wood and hooked setae. Syn.: *dualis* Peck.

43b. Setae absent

104. POLYPORUS SCHWEINITZII Fries. Context homogeneous, the hyphae 3–17 μ in diam.; cystidia present; pore surface greenish brown, becoming dark reddish brown with age. On the ground at the base of living gymnosperms or frequently sessile on the base of standing trees throughout except Ky., Okla., and Kans.

105. POLYPORUS SPATHULATUS (Hook.) Fries. Pores minute, 10–15 per mm.; upper surface shiny; spores 3–3.5 × 2–2.5 μ. On the ground under angiosperms in Fla.

39b. Sporophores sessile or effused-reflexed

44a. Spores hyaline or nearly so (compare also Nos. 120 and 123)

45a. Setae present

46a. Context duplex; persistently tomentose above

106. POLYPOROUS IODINUS Mont. On angiosperms in Fla. and La.

46b. Context homogeneous; becoming glabrous above

47a. Pores 5–8 per mm.

107. POLYPORUS GILVUS (Schw.) Fries. Upper surface of pileus becoming rough, tuberculate, azonate or somewhat zonate. On angiosperms or rarely on gymnosperms throughout. Intergrades with the next.

108. POLYPORUS LICNOIDES Mont. As in *P. gilvus* except pileus remaining smooth, multizonate. On angiosperms or rarely on gymnosperms in Ga., Fla., La., and Texas. Scarcely specifically distinct from *P. gilvus*. Var. *sublilacinus* (Ell. & Everh.) Overh., a perennial form, occurs in Ga. and Fla.

47b. Pores 3–5 per mm.

109. POLYPORUS RADIATUS Sow. ex Fries. Sporophore rather small, not over 2 cm. thick; spores ellipsoid, 4–6 × 3–4 μ. On angiosperms in Va., N. C., Tenn., and Mo. Var. *cephalanthi* Overh. has hooked setae, and occurs on Cephalanthus in La.

110. POLYPORUS DRYADEUS Pers. ex Fries. Sporophore large, 2–10 cm. thick; spores subglobose to globose, 5–8 μ in longest dimension. Usually produced at ground line of angiosperms, mostly oaks, in Md., D. C., W. Va., Va., N. C., Ga., Tenn., Ky., Mo., Ark., La., Texas, and Okla.

45b. Setae absent

111. POLYPORUS HYDNOIDES Swartz ex Fries. Pores 3–5 per mm.; pileus covered above with stiff hairs. On angiosperms in Fla., La., and Texas. Compare also No. 63.

112. POLYPORUS NIDULANS Fries. Pores 2–4 per mm.; pileus velvety to glabrous above; tissue cherry red or purple in KOH solution. On angiosperms in Del., Md., D. C., W. Va., Va., N. C., Tenn., Mo., La., and Kans. Syn.: *rutilans* Pers. ex Fries.

113. POLYPORUS CROCATUS Fries. Pores 6 per mm.; sporophore tan throughout. On angiosperms in Fla. and La.

114. POLYPORUS VINOSUS Berk. Pores 7–8 per mm.; sporophore dark purplish brown to brown-black throughout. On angiosperms and gymnosperms in N. C., S. C., Fla., Ala., and La.

44b. Spores distinctly colored

48a. Setae present

115. POLYPORUS GLOMERATUS Peck. Setal hyphae present in context and trama. On angiosperms in Del., N. C., and Ky.

116. POLYPORUS HISPIDUS Bull. ex Fries. Setal hyphae lacking; hirsute or hispid above; spores 7.5–10 × 6.5–9 μ. On angiosperms, especially oak, or rarely on gymnosperms, in Del., Md., D. C., W. Va., Va., N. C., Ga., Fla., Ala., Tenn., Mo., La., Texas, and Kans.

117. POLYPORUS CUTICULARIS Bull. ex Fries. Setal hyphae lacking; tomentose or fibrillose above; spores 5.5–8 × 4–5 μ. On angiosperms throughout except Md., Okla., and Kans.

48b. Setae absent

49a. Context with a central granular core

118. POLYPORUS DRYOPHILUS Berk. Pilei large, sometimes imbricate. On angiosperms in Va., N. C., Tenn., Mo., La., and Texas. Var. *vulpinus* (Fries) Overh. is smaller, hirsute or strigose, tomentose, with spores 4.5–7 × 3.5–4.5 μ; on Populus.

119. POLYPORUS GRAVEOLENS (Schw.) Fries. Pilei small, closely overlapping each other on a globose or cylindrical core. On angiosperms in Del., Md., D. C., W. Va., Va., N. C., S. C., Ga., Ala., Tenn., Ky., and Mo.

49b. Context without a central core
50a. Pores 2–3 per mm.

120. POLYPORUS FRUTICUM Berk. & Curt. Pileus encircling living twigs, soft and spongy; spores 4–5 × 3–3.5 μ. On angiosperms, especially Asimina, in Ga. and Fla. Syn.: *amplectans* (Murr.).

121. POLYPORUS TEXANUS (Murr.) Sacc. & Trott. On living tree trunks; pileus corky, drying rigid; spores 7–10 × 5–7 μ. On angiosperms in Texas.

122. POLYPORUS LUDOVICIANUS (Pat.) Sacc. & Trott. Forming imbricate masses of large sporophores, usually at base of trees; tough, drying rigid; spores 5–6 × 3.5–4 μ. On angiosperms in N. C., S. C., Ga., Fla., Ala., Ark., La., and Texas.

50b. Pores 4–8 per mm.

123. POLYPORUS CORROSUS (Murr.) Sacc. & Trott. Context duplex; pores 6–8 per mm.; spores 3–4 × 2–3 μ. On angiosperms in Fla.

124. POLYPORUS PORRECTUS (Murr.) Sacc. & Trott. Context homogeneous; pores 5–7 per mm.; spores globose, 4–5 μ in diam. On angiosperms in La.

125. POLYPORUS JUNIPERINUS (Murr.) Sacc. & Trott. Context homogeneous; pores 4–5 per mm.; spores 6–8 μ in diam. On Juniperus in Texas.

II. *FOMES* (Fries) Kickx

1a. Context pale brown to yellowish or reddish brown
2a. Spores distinctly colored
3a. Setae lacking or very rare
4a. Sporophore applanate; context duplex; spores 2.5–4 × 2.5–3 μ

1. FOMES RIBIS (Schum. ex Fries) Gill. On living angiosperms, usually Ribes and Crataegus, in Md., La., and Kans. Syn.: *langloisii* (Murr.).

4b. Sporophore applanate to ungulate; context homogeneous; spores 4–6 × 3.5–5.5 μ
5a. Sporophores light in weight; context hyphae conspicuously septate

2. FOMES SWIETENIAE (Murr.) Rick. Spores reddish brown; pores 5–8 per mm. On angiosperms in Fla.

3. FOMES FASTUOSUS (Lév.) Cooke. Spores reddish brown; pores 7–10 per mm. On angiosperms in Fla.

4. FOMES SUBLINTEUS (Murr.) Sacc. & Trott. Spores very dark brown to brown-black. On angiosperms in La. and Texas.

5b. Sporophore of medium weight; content hyphae inconspicuously septate

5. FOMES ROBINEAE (Murr.) Sacc. & D. Sacc. Pores 5–8 per mm. On living Robinia, occasionally on other angiosperms, in Md., D. C., W. Va., Va., N. C., Fla., Ala., Tenn., Ky., Mo., La., and Texas. Syn.: *rimosus* (Berk.) Cooke of many authors, not of Berk.

6. FOMES BADIUS (Berk.) Cooke. Pores 2–5 per mm. On angiosperms, usually living leguminous trees, in Texas. Intergrades with *F. robineae*.

3b. Setae infrequent to abundant
6a. Spores 2.5–4 × 2.5–4 μ.

7. FOMES JOHNSONIANUS (Murr.) Lowe. Subresupinate; setae mostly 19–24 μ long. On angiosperms in D. C., Va., Tenn., Mo., and La. Syn.: *densus* Lloyd sense of Overholts, not of Lloyd.

8. FOMES DEPENDENS (Murr.) Sacc. & Trott. Ungulate, usually pendent; setae 11–16 μ long. On angiosperms in Fla.

6b. Spores 4–5 × 3–5 μ

9. FOMES EVERHARTII (Ell. & Gall.) von Schrenk & Spauld. Pores 3–6 per mm.; spores dark reddish brown. On angiosperms, usually living, in Del., Md., W. Va., Va., N. C., Ga., Ala., Tenn., Ky., Mo., Ark. and Kans. Syn.: *praerimosus* (Murr.).

10. FOMES LINTEUS (Berk. & Curt.) Cooke. Pores usually 6–8 per mm.; spores usually nearly hyaline to pale golden brown. On angiosperms in Texas.

2b. Spores hyaline
7a. Context dark purple-brown, at least in part

11. FOMES MELANOPORUS (Mont.) Cooke. Dark purple-brown throughout; spores 4–5 × 2.5–3 μ. On angiosperms in Fla.

12. FOMES LIVIDUS (Kalchbr.) Sacc. Paler, the context usually only in part purple-brown; spores 5–7 × 3.5–5 μ. On angiosperms in Texas.

7b. Context yellowish or reddish brown
8a. Context composed of a thick horny layer enclosing a relatively soft inner tissue

13. FOMES FOMENTARIUS (L. ex Fries) Kickx. Pores about 3 per mm.; spores 17–20 × 5–6 μ. On living or dead angiosperms in W. Va., Va., N. C., and Tenn.

14. FOMES SCLERODERMEUS (Lév.) Cooke. Pores 4–6 per mm.; spores 8–13 × 3–4 μ. On dead or living angiosperms from N. C., Ga., Fla., Ala., Tenn., Miss., Ark., La., and Texas.

Syn.: *fasciatus* (Swartz) sense of Murrill, *marmoratus* (Berk. & Curt.).

8b. Context homogeneous or externally more or less indurated

9a. Setae usually more than 30 μ long

15. FOMES VITICOLA (Schw.) Lowe. Setae straight; spores cylindrical; sporophore resupinate or sessile and small. On angiosperms and gymnosperms in Md., W. Va., Va., N. C., Fla., Tenn., Ky., and Mo. Syn.: *tennuis* Karst., *isabellina* (Fries), *superficialis* (Schw.).

16. FOMES PINI (Thore ex Pers.) Overh. Setae straight; spores subglobose to globose, often becoming more or less brown in herbarium material; sporophore usually sessile, of moderate size. On gymnosperms in Del., Md., W. Va., Va., N. C., Ga., Fla., Ala., Tenn., Ky., Miss., Ark., La. and Kans.

17. FOMES ZEALANDICUS Cooke. Setae uncinate, at least in part. On angiosperms in S. C., Fla., and Tenn. Syn.: *extensus* (Lév.) Cooke sense of Overholts, not Léveille.

9b. Setae not more than 30 μ long

10a. Spores ellipsoid, 2.5–3 μ wide; setae subulate

18. FOMES TAXODII Murr. On cypress in Ga. and Fla.

10b. Spores ovoid to globose, 3–8 μ wide; setae ventricose

19. FOMES ROBUSTUS Karst. Context bright yellowish brown; basidia 9–11 μ in diam.; spores 4–8 μ in diam.; setae rare, 16–19 μ long. On angiosperms and gymnosperms in Del., Md., D. C., W. Va., Va., N. C., S. C., Fla., Ala., Miss., Tenn., Mo., La., and Texas. Syn.: *bakeri* (Murr.), *calkinsii* (Murr.), *texanus* (Murr.).

20. FOMES CONCHATUS (Pers. ex Fries) Gill. Context dull reddish or yellowish brown; basidia 4–6 μ in diam.; spores 4–5 μ in diam.; setae 18–30 μ long. On angiosperms in Md., W. Va., N. C., Fla., Tenn., Mo., Ark., and Texas. Syn.: *densus* Lloyd.

21. FOMES IGNIARIUS (L. ex Fries) Kickx. Context dark reddish brown; basidia 6–7.5 μ in diam.; spores 4–5 μ in diam.; setae 11–14 μ long. On living or dead angiosperms in Md., W. Va., Va., N. C., Tenn., Mo., Ark., and Kans. Syn.: *nigricans* (Fries) of American authors.

22. FOMES POMACEUS (Pers.) Lloyd. A dwarf form of *F. igniarius* on drupaceous hosts in Md., D. C., W. Va., Va., N. C., S. C., Ga., Ala., Tenn., Ky., Mo., and Kans. Its usual habitat on small branches may account for its small size. Syn.: *fulvus* (Scop. ex Fries).

1b. Context yellowish, becoming brick red

23. FOMES DEMIDOFFII (Lév.) Cooke. On living Juniperus in Md., Tenn., Ky., Mo., and Texas. Syn.: *earlei* (Murr.), *juniperinus* (von Schrenk).

1c. Context pink or rose

24. FOMES FRAXINEUS (Bull. ex Fries) Cooke. Spores ovoid to subglobose; context often fading in the herbarium. On angiosperms in Fla., Ala., Ark., and La.

25. FOMES FEEI (Fries) Lowe. Spores oblong-ellipsoid; pores 5–6 per mm. On angiosperms in Fla.

26. FOMES CAJANDERI Karst. Spores cylindrical; pores 3–5 per mm. On gymnosperms or rarely on angiosperms in Md., W. Va., Va., N. C., Ga., Fla., Ala., Tenn., Ky., and Ark. Syn.: *subroseus* (Weir).

1d. Content white to cream

11a. Context hyphae septate

27. FOMES CONNATUS (Weinm.) Gill. Incrusted cystidia present; pores 4–5 per mm. On angiosperms in Del., Md., W. Va., Va., N. C., Ga., Tenn., Ky., and Mo. Syn.: *populinus* (Schum.) sense of Murrill.

28. FOMES ULMARIUS (Sow. ex Fries) Gill. Cystidia not incrusted; pores 5–8 per mm. On angiosperms in Ga., Fla., Miss., Ark., La., and Texas. Syn.: *geotropus* Cooke of American authors.

11b. Context hyphae apparently nonseptate

12a. Spores cylindrical

29. FOMES SCUTELLATUS (Schw.) Cooke. Sporophore small. On Alnus and other angiosperms in Del., W. Va., N. C., Ga., Fla., and Tenn.

12b. Spores ellipsoid to globose

13a. Spores often truncate at one end

30. FOMES FRAXINOPHILUS (Peck) Cooke. Pores 2–3 per mm.; sporophore becoming large; spores 7–11 μ long. On living and dead angiosperms in W. Va., Va., Tenn., Ky., Mo., Ark., and Kans.

31. FOMES OHIENSIS (Berk.) Murr. Pores 3–5 per mm.; sporophore remaining small; spores 10–13 μ long. On angiosperms in W. Va., Va., N. C., Tenn., Ky., Mo., and Okla.

32. FOMES UNITUS (Pers.) Lowe. Usually resupinate or nearly so; pores 5–8 per mm.; spores 4–7 μ long. On angiosperms or gymnosperms in Del., Md., W. Va., Va., N. C., S. C., Ga.,

Ala., Ky., Mo., Ark., and La. Syn.: *cremor* (Berk. & Curt.) *dryina* (Berk. & Cooke), *limitata* (Berk. & Curt.), *medulla-panis* (Pers.), *tomentocincta* (Berk. & Rav.).

13b. Spores rounded at both ends

33. FOMES PINICOLA (Swartz ex Fries) Cooke. Sporophore usually sessile, thick; spores 5–7 μ long. On gymnosperms and angiosperms in W. Va., Va., N. C., Tenn. and Mo.
34. FOMES ANNOSUS (Fries) Karst. Sporophores often resupinate to effused-reflexed, thin; spores 4.5–5 μ long. On gymnosperms and rarely on angiosperms throughout except not recorded from S. C., Ky., and La.

III. *TRAMETES* Fries

1a. Context distinctly brown

2a. Spores allantoid; sporophores usually resupinate

1. TRAMETES CARBONARIA (Berk. & Curt.) Overh. Pores usually hexagonal; spores 7–10 × 2.5–4 μ; hyphae with abundant clamp connections. Usually on charred wood of gymnosperms in Ga., Fla., Tenn., and Mo.

2b. Spores cylindrical, straight; clamp connections rare or absent on principal context hyphae

3a. Pileus glabrous or tomentose, not hispid

2. TRAMETES MALICOLA Berk. & Curt. Context tissue light brown; spores 8.5–10.5 × 3–3.5 μ. On angiosperms and rarely on gymnosperms, in D. C., W. Va., N. C., Ga., Tenn., and La.
3. TRAMETES ODORATA Wulf. ex Fries. Context tissue dark yellowish brown or reddish brown; spores 10–14 × 3–4 μ. On gymnosperms and rarely on angiosperms in W. Va., Va., Fla., and Tenn. Syn.: *americana* Overh.

3b. Pileus coarsely hispid

4a. Upper hispid layer separated from the lower context by one or more thin black layers

4. TRAMETES MOLLIS (Sommerf.) Fries. Spores cylindrical, 7–8.5 × 3–3.5 μ. On angiosperms in D. C., W. Va., N. C., Tenn., and Ky.

4b. Upper hispid layer continuous with the lower context, black layer not present

5. TRAMETES HISPIDA Bagl. Spores 11–14 × 3–4 μ; context thick, appearing duplex because of soft upper layer. On angiosperms in Mo., Ark., La., Texas, and Okla.
6. TRAMETES TROGII Berk. Spores 8–10 × 2–2.5 μ; context thin, not appearing duplex. On angiosperms in Md.

1b. Context whitish to yellowish or very pale brownish

5a. Pores usually 2–5 per mm.

6a. Sporophores usually sessile

7. TRAMETES SUAVEOLENS Fries. Spores fusiform, 8.5–10.5 × 3–3.5 μ. On living angiosperms in Ga. and Mo.
8. TRAMETES CUBENSIS (Mont.) Sacc. Sporophores applanate, thin; included by Overholts (1953) but better placed in Polyporus. On angiosperms in Fla. and La.

6b. Sporophores usually resupinate

9. TRAMETES SERIALIS Fries. Spores cylindrical, 6.5–9 × 2.5–3.5 μ. Usually on gymnosperms and rarely angiosperms in Md., W. Va., N. C., Ala., Tenn., Mo., Ark., La., and Kans.
10. TRAMETES RIGIDA Berk. & Mont. Spores cylindrical, 7–12 × 3–5 μ; hyphal pegs present. On angiosperms in D. C., S. C., Fla., Ala., Tenn., Mo., La., and Texas.

5b. Pores usually 1–2 per mm. or often larger than 1 mm. in diam.

7a. Upper surface of pileus reddish brown

11. TRAMETES VARIIFORMIS Peck. Spores 7–10 × 3–4 μ. On gymnosperms in Tenn.

7b. Upper surface of pileus white to tan or becoming blackish

12. TRAMETES HETEROMORPHA (Fries) Bres. Upper surface usually ivory white; spores 10–16 × 3.5–4 μ. On gymnosperms in Va., N. C., Ala., Tenn., and Mo. Syn.: *hexagoniformis* (Murr.).
13. TRAMETES SEPIUM Berk. Upper surface pale brownish to blackish; spores 8–11.5 × 2.5–4 μ. On angiosperms throughout except Del., S. C., and Okla.

IV. *PORIA* Pers. ex S. F. Gray emend. Cooke

Section 1. SPOROPHORES WHITE OR BRIGHTLY COLORED, AT LEAST WHEN FRESH, NOT BROWN AND THE TISSUE NOT BLACKENING IN KOH SOLUTION (for brown species see No. 85).

1a. Pores arising as papillae which open with age, sporophore becoming poroid

1. POROTHELEUM FIMBRIATUM (Pers. ex Fries) Fries. Sporophore membranous, rhizomorphic. On angiosperms and gymnosperms in Md., W. Va., Va., N. C., S. C., Fla., Ala., Tenn., Ky., Mo., and Ark. The genus has been fully treated by Cooke in Mycologia **49:** 680–693. 1957.

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1b. Pores open and hymenium exposed from the first

2a. Basidia cruciately divided (genus Aporpium)

2. APORPIUM CARYAE (Schw.) Teix. & Rogers. On angiosperms along the Atlantic Coast and in Ky. and La. Syn.: *canescens* Karst., *gilvescens* of American authors, not Bres.

2b. *Basidia nonseptate, restricted to the base of the tubes* (genus Porogramme)

3. POROGRAMME FULIGO (Berk. & Br.) Pat. Pore surface blue. Erroneously reported previously; should occur in the subtropical areas. Syn.: albocincta (Cooke & Massee), *aurantiotingens* (Ell. & Macbr.).

2c. Basidia nonseptate, lining base and sides of tubes (genus Poria)

3a. Context hyphae with simple septa. (In some species the context hyphae under well-developed tubes will appear nonseptate. The hyphae of the margin should then be examined.)

4a. Some of the context hyphae much inflated, up to 20 μ in diam.

4. PORIA INFLATA Overh. Pores 3–5 per mm.; spores 4–5 × 2.5–3 μ. On angiosperms in Mo.

5. PORIA MAGNAHYPHA Overh. Pores 1 mm. broad or wider; spores 8–10 × 3.5–4 μ; tubes tough when dry. On angiosperms in Tenn.

6. PORIA COCOS (Schw.) Wolf. Pores 1–3 per mm.; spores 7–11 × 2.5–3 μ; tubes fragile when dry. Associated with a sclerotium found in soil in Del., Md., Va., N. C., S. C., Ga., Fla., Ala., Miss., Tenn., Ky., Mo., Ark., Texas, and Kans. Sporophores readily produced from sclerotia; very rarely fruiting on wood.

4b. Context hyphae more or less uniform in diameter and rarely exceeding 8 μ

5a. Spores ellipsoid to globose

6a. Cystidia present

7a. Cystidia capitate incrusted, short

7. PORIA CORTICOLA (Fries) Cooke. Context hyphae uniformly 3–4 μ in diam. On angiosperms in Md., W. Va., Va., N. C., S. C., Fla., Ala., Miss., Mo., Ark., and La. Syn.: ? *salviae* (Berk. & Curt.)—type sterile and myriadoporous, ? *vesiculosa* (Berk. & Curt.)—type sterile and myriadoporous.

8. PORIA AMBIGUA Bres. Context hyphae variable, 3–8 μ in diam. On angiosperms in Md., D. C., Va., N. C., S. C., Ga., Fla., Ala., Miss., Tenn., Ky., Mo., Ark., and Texas. Syn.: *cokeri* Murr., *lacerata* Murr.

7b. Cystidia clavate incrusted, long

9. PORIA CARNEOPALLENS (Berk.) Cooke. Tubes cartilaginous; pore surface more or less pinkish; spores often with flattened sides and appearing more or less triangular, 3.5–4 × 2.5–3.5 μ. On angiosperms in Fla. and La. *P. vincta* (Berk.) Cooke in tropical America is similar and uncertainly distinct, as type is sterile.

10. PORIA LACTEIMICANS Murr. Tubes rather fragile or papery; pore surface white to cream; pores 7–10 per mm.; spores ellipsoid to oval, 2–3 × 1.5–2.5 μ. On angiosperms in Fla. The cystidia have been overlooked previously. Syn.: *floridae* Murr.

11. PORIA SIMILIS Bres. Tubes fragile; pore surface white to cream; pores 3–5 per mm.; spores 2.5–5 × 2.5–3.5 μ. On angiosperms in Mo.

6b. Cystidia absent

8a. Spores spiny

12. PORIA TRACHYSPORA Bourd. & Galz. On angiosperms in N. C. Sporophore is poroid; otherwise plant is misplaced in Poria. Pilát places it in the genus Lindtneria.

8b. Spores smooth

9a. Sporophore soft, drying soft or fragile

10a. Spores oblong-ellipsoid to ellipsoid

13. PORIA FATISCENS (Berk. & Rav.) Cooke. Tubes drying rigid, fragile; pores 2–4 per mm.; spores 3–4 μ long. On angiosperms and gymnosperms in D. C., W. Va., Va., N. C., S. C., Fla., Ky., and Mo. Syn.: *fagicola* Bres., *semitincta* (Peck).

14. PORIA CUBITISPORA Murr. Tubes drying rigid and fragile; pores 7–8 per mm.; spores 2.5–3 μ long. On gymnosperms in Fla.

10b. Spores broadly ellipsoid to subglobose

11a. Pores 2–4 per mm.

15. PORIA TERRESTRIS (DC.) Sacc. Rhizomorphic, membranous and readily separable; tubes drying distinctly yellowish or sometimes pinkish. On angiosperms and gymnosperms in N. C. Syn.: *parksii* Murr.

16. PORIA SUBAMBIGUA Bres. Not rhizomorphic, adnate; tubes whitish to tan when dry. On angiosperms and gymnosperms in Md. and La. Syn.: *flaccida* Overh.

11b. *Pores* 5–6 per mm.

17. PORIA CHRYSOBAPHA (Berk. & Curt.) Cooke. Spores pale yellowish brown; pore surface "golden yellow, inclining to olive" (Berkeley and Curtis); tubes rigid and rather fragile when dry. Known only from the type, a small inadequate specimen from Alabama.

18. PORIA DIOSPYRI Baxt. [Spores hyaline; pore surface white or slightly sulphureus. Known only from the type from Okla.].

9b. Sporophore drying tough, corky or cartilaginous

12a. Context hyphae 2–5 μ in diam.

19. PORIA DISCOLOR Overh. Pores 3 per mm. On angiosperms in Tenn.

20. PORIA ALBOSTYGIA (Berk. & Curt.) Lloyd. Pores 6–10 per mm. On angiosperms in Fla. Probably a resupinate condition of a species of Polyporus. Very similar to the next species.

12b. Context hyphae mostly 5–8 μ in diam.

21. PORIA NIGRESCENS Bres. Context fibrous to corky; pore surface pinkish when fresh, darkening where bruised; associated with a uniform white rot. On angiosperms and gymnosperms in W. Va., Va., N. C., S. C., Fla., Tenn., Ark., and La.

22. PORIA UNDATA (Pers.) Bres. Context drying cartilaginous; pore surface white, drying pinkish; associated with a conspicuous white pocket rot. On angiosperms in Va., N. C., Ga., Fla., Miss., and La. Syn.: *holoseparans* Murr.

23. PORIA SANGUINOLENTA (Alb. & Schw.) Sacc. Context drying cartilaginous, whole sporophore often dark on drying. On angiosperms and gymnosperms in Fla. Syn.: *decolorans* (Schw.).

5b. Spores cylindrical, short-oblong or allantoid

13a. Base of tubes at first isolated from each other, joined by radial extension, i.e., cupulate

24. PORIA RHODELLA (Fries) Bres. Spores 3–5 μ long; pore surface extremely variable in color, whitish to gray, or greenish, or rosy. On angiosperms and gymnosperms in Ala., Ky., and La. Syn.: *griseoalba* (Peck),? *subbadia* Murr.—type sterile, *viridans* (Berk. & Br.).

25. PORIA PURPUREA (Fries) Cooke. Spores 5–9 × 1.5–2.5 μ; pore surface more or less reddish when dry. On angiosperms and gymnosperms in W. Va., N. C., S. C., Ala., Tenn., Ky., and Kans. Very similar to the next except for color.

26. PORIA RETICULATA (Fries) Cooke. Spores 6–10 × 2.5–3.5 μ; pore surface white to cream when dry. On angiosperms and gymnosperms in W. Va., N. C., and Fla.

13b. Tubes formed on a continuous mycelial mat

14a. Pores 3–4 per mm.

27. PORIA TAXICOLA (Pers.) Bres. Pores 3–4 per mm.; on gymnosperms in Tenn. and, according to Baxter, in S. C. and La. Syn.: *rufa* (Schrad. ex Fries).

14b. Pores 5–8 per mm.

28. PORIA SPISSA (Schw.) Cooke. Pore surface orange, drying dark red; spores allantoid; mild. On angiosperms in Del., D. C., W. Va., Va., N. C., S. C., Ala., Tenn., Ky., and Mo. Syn.: *laetifica* (Peck), ? *oxydata* (Berk. & Curt.)—type sterile.

29. PORIA ALACHUANA Murr. Pore surface cream when dry; spores short-oblong; context hyphae 3–4.5 μ in diam.; disagreeably resinous. On angiosperms in Fla., Miss., Ark., and La.

30. PORIA FERRUGINICINCTA Murr. Pore surface sordid yellowish brown when dry; spores short-oblong; context hyphae 4–8 μ in diam.; disagreeably resinous. On angiosperms in Fla.

3b. Context hyphae with clamp connections, rarely with simple septa as well

15a. Spores becoming more or less brown at maturity

31. PORIA INCRASSATA (Berk. & Curt.) Burt. Pore surface becoming more or less brown in age and on drying; some of context hyphae distinctly brown. On gymnosperms, especially of building timbers, in D. C., Va., S. C., Ga., Fla., Ala., Tenn., Miss., Ky., La., Texas, and Okla.

15b. Spores hyaline, echinulate or longitudinally striate

16a. Spores oval to globose, 2.5–6 × 2–5 μ

17a. Sporophore drying soft-leathery

32. PORIA AVELLANEA Bres. Spores 3–5 × 2.5–3.5 μ. On angiosperms in S. C. and Fla. Syn.: *heteromorpha* Murr.

33. PORIA LENTA Overh. & Lowe. Spores 5–6 × 4–5 μ. On gymnosperms in Tenn.

17b. Sporophore drying soft-cottony or fragile

34. PORIA CANDIDISSIMA (Schw.) Cooke. Tubes cottony-soft or fragile, the pores 3–4 per mm.; noncystidiate. On angiosperms and gymnosperms in Va., N. C., S. C., Tenn., Mo., and La. Syn.: *hymenocystis* (Berk. & Br.) and *subtilis* (Schrad. ex Fries) of European determinations.

Perhaps only a form of this which differs in that it has oblong spores occurs in N. C. and S. C. Except that the basidia are not urniform, it agrees very well with *Trechispora albolutea* var. *xystrospora* Bourd. & Galz.

35. PORIA REGULARIS Murr. Tubes very soft, the pores 5 per mm.; cystidiate. On angiosperms in N. C., S. C., and La. Syn.: *arachnoidea* Murr., *submollusca* Murr.

16b. Spores oblong, 8–16 × 3–7 μ

36. PORIA PAPYRACEA (Schw.) Cooke. Spores 13–16 × 5.5–7 μ; pores 2–2.5 per mm. On angiosperms and gymnosperms in Va., N. C., S. C., Fla., Ala., and Ky. Syn.: *barbaeformis* (Berk. & Curt.).

37. PORIA ALABAMAE (Berk. & Cooke) Cooke. Spores 8–14 × 3–7 μ; pores 4 per mm. On angiosperms in Fla. and Miss.

15c. Spores hyaline, smooth

18a. Pore surface pink, lavender, orange, or red when dry

19a. Cystidia present

38. PORIA EUPORA (Karst.) Cooke. On angiosperms in Va., N. C., Tenn., Mo., and La. Syn.: *attenuata* (Peck).

19b. Cystidia lacking

20a. Pores 2–4 per mm.

39. PORIA ATRORUBENS Baxt. [Spores 4 × 1.5–2 μ; white, turning garnet where bruised, drying reddish brown. On angiosperms in Ark.] The relation of this species to others that turn red on bruising is uncertain.

40. PORIA SALMONICOLOR (Berk. & Curt.) Cooke. Spores 4–6 × 2–2.5 μ; pore surface orange, drying livid red or purplish; soft, waxy, drying hard and brittle. On gymnosperms in S. C. and Fla. Not a synonym of *P. spissa*. Syn.: *rubens* Overh. & Lowe.

41. PORIA BOMBYCINA (Fries) Cooke. Spores 5–7 × 3–4 μ; pore surface very variable when fresh, drying lavender to pinkish tan; soft-fibrous, drying fibrous-fragile. On gymnosperms in W. Va. according to Baxter.

20b. Pores 4–9 per mm.

42. PORIA MUTANS Peck. Spores broadly ellipsoid to subglobose; tubes drying agglutinated, rigid; pores 4–6 per mm. On chestnut in Md., D. C., W. Va., Va., N. C., Ala., Tenn., and Ky.

43. PORIA BORBONICA Pat. Spores broadly ellipsoid to subglobose; tubes drying somewhat corky; pores 8–9 per mm. On angiosperms in Fla. and La. Syn.: *cinereicolor* Murr.

44. PORIA RHOADSII Murr. Spores oblong to oblong-ellipsoid, 3–4 × 1.5–2 μ; tissue violaceous then decolorate in KOH solution; tubes drying tough; pores 4–6 per mm. On angiosperms in Fla. Syn.: *ossea* Baxt.

45. PORIA PHLEBIAEFORMIS Berk. Spores oblong-ellipsoid, 4.5–5.5 × 3–3.5 μ; tissue persistently rose-purplish in KOH solution; tubes drying fragile; pores 5–6 per mm. On angiosperms in Fla.

18b. Pore surface drying white to cream or yellow or tan

21a. Cystidia present

22a. Spores short-oblong or ellipsoid to subglobose

46. PORIA FIMBRIATELLA (Peck) Sacc. Tough-membranous, rhizomorphic; cystidia incrusted. On angiosperms in Tenn., determination not wholly certain.

47. POLYPORUS VERSITALIS (Berk.) Rom. Papery-corky, not rhizomorphic; cystidia capitate incrusted; grayish-vinaceous, drying pale brown; pores 1–3 per mm. On angiosperms and gymnosperms in Fla. This species was formerly confused with *Poria cavernulosa* (Berk.) Cooke.

48. PORIA SERICEOMOLLIS (Rom.) Baxt. Corky-fragile, not rhizomorphic; cystidia capitate-incrusted; white to cream; bitter. On gymnosperms or rarely on angiosperms in N. C., S. C., Fla., and Tenn. Syn.: *asiatica* Pilát.

49. PORIA EYREI Bres. Corky-fragile, not rhizomorphic; cystidia capitate incrusted; pale tan; mild. On angiosperms in Md.; not previously reported from North America. The species appears to be a cystidiate form of *P. versipora*.

22b. Spores cylindrical

50. PORIA LUTEOALBA (Karst.) Sacc. Cystidia large, heavily incrusted; spores 4–5 × 1–2 μ. On gymnosperms in Del., Va., N. C., Fla.,

Tenn., and Miss. Syn.: *sinuascens* Pilát.

51. PORIA LATITANS Bourd. & Galz. Cystidia imbedded, not incrusted, hyphoid to subventricose, apparently solid; spores 3–5 × 0.5–1 μ. On gymnosperms and angiosperms in Fla., Miss. and Ark.; not previously reported from North America.
52. PORIA RIMOSA Murr. Similar to *P. latitans* except the cystidia distinctly projecting, slender-conical, thin walled, the spores 1.5–2 μ wide. On Juniperus in Texas and Okla.

21b. Cystidia absent

23a. Spores ellipsoid to globose

24a. Pore surface or rhizomorphs yellow

53. PORIA ALBOLUTESCENS (Rom.) Egel. Drying soft; pores 3–4 per mm.; spores 3.5–4 × 2–2.5 μ. On gymnosperms in N. C., Tenn., and La. Syn.: *grandis* Overh.
54. PORIA RADICULOSA (Peck) Sacc. Drying rigid; pores 1–3 per mm.; spores 5–8 × 2.5–3.5 μ. On gymnosperms and angiosperms in N. C., Fla., Miss., Tenn., and La. Syn.: *flavida* Murr., [?*luteofibrata* Baxt.], *subradiculosa* Murr.
55. PORIA FLAVIPORA Berk. & Curt. Drying rigid; pores 4–6 per mm.; spores 3.5–5 × 2.5–3.5 μ. On angiosperms in Fla. The interrelations of this inadequately known species are in doubt. Dried specimens retain little of the color indicated by the specific name.

24b. Pore surface and rhizomorphs white to cream

25a. Sporophore membranous, rhizomorphic

56. PORIA VAILLANTII (DC. ex Fries) Cooke. Drying soft; spores 5–7 μ long; mild. On gymnosperms in Md., D. C., Va., N. C., Tenn., and Mo.
57. PORIA OVERHOLTSII Pilát. Drying fragile; spores 4–7 μ long; bitter. On angiosperms and gymnosperms in Va., N. C., Fla., and Tenn.
58. PORIA MYCELIOSA Peck. Drying soft; spores somewhat oblong, 3–4 × 2.5–3 μ. On gymnosperms in Va., N. C., and Tenn.
59. PORIA MOLLUSCA (Pers. ex Fries) Cooke. As in *P. myceliosa* except spores subglobose to globose, 3–4 μ in diam. On gymnosperms and angiosperms in Va., Fla., and Ark.
60. PORIA HUMILIS Murr. Drying tough-membranous; spores 5–6 μ long; mild. On gymnosperms and angiosperms in Va. and Tenn., identification not wholly certain. Syn.: *incrustans* (Berk. & Curt.).

25b. Sporophore adnate, not membranous and not rhizomorphic

26a. Sporophore bitter; perennial

61. PORIA CRASSA (Karst.) Sacc. Pores 5–6 per mm.; spores 4–5 × 3–3.5 μ. On gymnosperms in N. C.
62. PORIA OLERACEA Davids. & Lomb. Pores 2–4 per mm.; spores 5–7 × 2.5–3 μ; tubes somewhat chalky when dry; context hyphae frequently branched, 2–4 μ in diam. On angiosperms in Md., N. C., and Tenn.
63. PORIA FEROX Long & Baxt. Much as in *P. oleracea* but with soft-corky tubes; context hyphae 1.5–3 μ in diam. On gymnosperms in Ark. The type closely resembles *Fomes unitus*, differs in having larger pores and seldom branched context hyphae.

26b. Sporophore mild; annual

27a. Context soft or fibrous-fragile when dry

64. PORIA ANEIRINA (Sommerf.) Cooke. Pores 1–3 per mm. On angiosperms, especially Populus, in Ala.
65. PORIA VERSIPORA (Pers.) Rom. Pores 3–5 per mm.; context hyphae 3–4 μ in diam., rather thin walled and with abundant clamps; spores 4–7 × 2.5–4 μ. On angiosperms throughout except Ga. Syn.: *ochracea* Murr.
66. PORIA CONFERTA Overh. Quite similar to *P. versipora* except context hyphae thick walled and with clamps usually present only on marginal hyphae. On hardwoods in Tenn.
67. PORIA CALKINSII Murr. Pores 3–4(–6) per mm.; context hyphae mostly 1.5–3 μ in diam., some however 4–7 μ in diam. and such hyphae constituting the trama; spores 3–4 × 2.5–3 μ. On angiosperms in Fla.; known only from the type.
68. PORIA FISSILIFORMIS Pilát. Tubes drying glassy-fragile. On angiosperms in Mo. No. 88, *Polyporus semisupinus*, is often resupinate and very similar except tubes of that species dry tough-corky.

27b. Context firm to hard, or fibrous-tough

28a. Spores rounded on both ends

69. PORIA DISTORTA Murr. Spores 3–4 × 2.5 μ; drying as a thin, tough membrane. Known

only from the type from N. C. on angiosperms, surely an abnormal specimen. The sporophore may be a resupinate condition of a species of Polyporus.

70. PORIA ELACHISTA (Berk.) Cooke. Spores 4–5 × 2–2.5 μ; tubes apparently drying waxy-fragile but texture uncertain as only specimen is impregnated with mounting glue. On rotten wood (? of angiosperms) in S. C.; inadequately known from minute specimens of type material. Syn.: *minima* (Rav.).

28b. Spores frequently truncate at one end

71. PORIA SUBACIDA (Peck) Sacc. Spores 4–5.5 μ long; pores 2–4 per mm.; context hyphae highly variable, 1.5–5 μ in diam. On angiosperms and gymnosperms in Md., W. Va., Va., N. C., S. C., Fla., Tenn., Ala., Ky., Mo., Ark., La., and Kans. Syn.: *omaema* Berk. This species integrades with the next.

72. PORIA TENUIS (Schw.) Cooke. Spores 5–7 μ long; pores 2–5 per mm. On angiosperms in Md., W. Va., Va., N. C., Ga., Ala., Tenn., Ky., Mo., Ark., La., and Texas. Syn.: *beaumontii* Berk. & Cooke. The yellow forms of this have been called *P. pulchella* (Schw.) Cooke and *P. holoxantha* Berk. & Cooke.

73. FOMES UNITUS (Pers.) Lowe. Spores 4–7 μ long; pores 5–8 per mm. Usually resupinate; on angiosperms nearly throughout; see under Fomes.

23b. Spores cylindrical, oblong or allantoid

29a. Sporophore drying tough

30a. Pores 1–4 per mm.

74. PORIA RANCIDA Bres. Bitter; tubes when dry rather soft and fragile; white, drying brownish. On angiosperms and gymnosperms in Tenn. Syn.: *cognata* Overh.

75. PORIA CRUSTULINA Bres. Mild; tubes when dry rigid and rather tough; usually more or less yellowish. On gymnosperms in Tenn.

30b. Pores 4–7 per mm.

76. PORIA ALUTACEA Lowe. Rhizomorphic; membranous; spores 2.5–3.5 × 1.5 μ. On angiosperms and gymnosperms in N. C. and Tenn.

77. PORIA CINERASCENS Bres. Nonrhizomorphic; adnate; spores 4–7 × 1.5–2.5 μ; pores 4–5 per mm.; pore surface drying more or less sordid. On gymnosperms in Va., Ala., Tenn., and Ark. Syn.: *subavellanea* Murr.; *subfuscoflavida* (Rostk.) of American determinations.

78. PORIA SUBINCARNATA (Peck) Murr. Nonrhizomorphic; spores 3.5–5 × 1–2 μ; pores 5–7 per mm., the pore surface with a pinkish tinge. On gymnosperms and angiosperms in Va., N. C., and Tenn.

79. PORIA LENIS (Karst.) Sacc. Nonrhizomorphic; pores 5–7 per mm.; spores typically lunate, 3.5–4 × 1–1.5 μ. On gymnosperms and angiosperms in W. Va., Va., N. C., Fla., Ala., and Tenn.

29b. Sporophore drying fragile or very soft

31a. Pore surface more or less yellowish, at least when fresh

80. PORIA PANNOCINCTA (Rom.) Lowe. Tubes drying rigid, glassy; context with a thin resinous line just under the tubes; slowly bitter. On angiosperms in Tenn. and Ga. Syn.: [*?viridiuscula* Baxt.], *zameriensis* (Pilát).

81. PORIA XANTHA (Fries) Cooke. Tubes drying chalky; context homogeneous; intensely bitter. On gymnosperms and angiosperms in W. Va., Va., N. C., and S. C.

31b. Pore surface white

82. PORIA VAPORARIA (Pers. ex Fries) Cooke. Pores 1–3 per mm.; mild. On gymnosperms in Va., N. C., S. C., Ga., and Ala.

83. PORIA SUBVERMISPORA Pilát. Pores 2–4 per mm.; bitter. On angiosperms and gymnosperms in Md., Ga., and Mo. Syn.: *notata* Overh., [*?quercuum* Baxt.].

84. PORIA VULGARIS (Fries) Rom. Pores 4–6 per mm.; mild; context often with a gelatinous layer next the substratum. On gymnosperms in N. C. and Fla. according to Baxter.

Section 2. SPOROPHORE SOME SHADE OF BROWN AND THE TISSUE BLACKENING IN KOH SOLUTION.

32a. Spores distinctly brown (compare also 99. *P. melleopora*)

85. PORIA INERMIS Ell. & Everh. Spores 5–6 × 4–5 μ. On angiosperms—especially Ilex, Nemopanthus, and Rhus—in D. C., Va., Ga., Fla., Ala., Miss., Mo., La., and Kans.

86. PORIA UMBRINELLA Bres. Spores 3.5–4.5 × 2.5–4 μ; pores 6–8 per mm. On angiosperms in Fla. and La. Syn.: *floridana* (Murr.), *langloisiana* (Murr.). A variable fungus, the tubes

sometimes translucent when dry, sometimes not.

32b. Spores greenish yellow in mass

87. PORIA ANDERSONI (Ell. & Everh.) Neuman. Sporophore formed within the outer layers of wood, these splitting off, usually exposing a conspicuous spore deposit. On angiosperms in Del., Md., N. C., Tenn., Mo., Ark., and Texas.

32c. Spores hyaline, or in age becoming at most pale brown

33a. Setae usually frequent to abundant

34a. Spores cylindrical

88. PORIA FERRUGINEO-FUSCA Karst. Trama made up wholly or largely of setal hyphae; pores 4–6 per mm.; spores 4–5 × 1.5–2 μ. On gymnosperms in Ala.; record somewhat uncertain as specimen is sterile.

89. PORIA FERREA (Pers.) Bourd. & Galz. Trama of ordinary hyphae; pores 4–6 per mm.; spores 5–8 × 2–2.5 μ; setae 25–40 × 6–8 μ. On angiosperms in Md., W. Va., Va., Fla., and Tenn.

90. FOMES VITICOLA (Schw.) Lowe. Often resupinate; trama of ordinary hyphae; spores 6–8.5 × 1.5–2 μ; pores 2–4 per mm.; setae 25–80 × 5–11 μ. On gymnosperms and angiosperms, rather widely distributed. See under Fomes.

34b. Spores oblong-ellipsoid to subglobose

35a. Setae large, 25–50 or more × 5–10 μ

91. PORIA FERRUGINOSA (Schrad. ex Fries) Karst. Spores ellipsoid, 4–6 × 2.5–4 μ. On angiosperms and gymnosperms in W. Va., Va., N. C., Ala., Tenn., Ky., Mo., and La.

35b. Setae rarely exceeding 25 μ in length

36a. Spores large, 8–10 × 6–7.5 μ

92. PORIA OBLIQUA (Pers. ex Fries) Karst. Sporophore forming within the outer layers of the wood, these splitting off. On angiosperms in W. Va. Forms sterile conks on living trees; after death of host, sporophores formed; these usually quickly destroyed by insects.

36b. Spores smaller, not over 6 μ in longest dimension

93. PORIA PUNCTATIFORMIS Murr. Spores oblong-ellipsoid, 4.5–6 × 1.5–2.5 μ; pores 6–7 per mm. On Quercus in Fla.

94. PORIA LAEVIGATA (Fries) Karst. Spores broadly oval, 3.5–4.5 × 2.5–3.5 μ; pores 8–10 per mm.; perennial; context tissue dark brown. On angiosperms in D. C., W. Va., Va., N. C., Fla., Ala., Ky., Mo., La., and Okla. This is the resupinate condition of *Fomes igniarius*.

95. PORIA LUDOVICIANA (Murr.) Sacc. & Trott. As in *P. laevigata* except context tissue pale reddish brown and setae somewhat more slender. On angiosperms in La. The species differs from *P. laevigata* by such slight variations that it may well be a synonym.

96. PORIA SPICULOSA Campb. & Davids. Virtually impossible to separate from *P. laevigata* by its sporophore morphology; culturally said to be quite different. On angiosperms in Del., Va., N. C., S. C., and Fla.

33b. Setae lacking or rare

97. PORIA PUNCTATA (Fries) Karst. Spores 5–8 μ in largest dimension; tissue reddish brown; perennial. On angiosperms and gymnosperms throughout. This is the resupinate form of *Fomes robustus*. Syn.: *dryophila* (Murr.), *earleae* (Murr.), *juniperina* (Murr.), *langloisii* (Murr.), *tsugina* (Murr.), and *hartigii* (Bres.).

98. PORIA NIGRA (Berk.) Cooke. Spores 3–5 × 2–3 μ; sporophore chocolate brown throughout. On angiosperms in W. Va., N. C., S. C., Ala., Ky., Mo., and Kans.

99. PORIA MELLEOPORA (Murr.) Sacc. & Trott. Spores becoming pale brownish, 4–5 × 2.5–3.5 μ; context hyphae 3–5 μ in diam.; sporophore yellowish or reddish brown. On angiosperms in La. Similar to *P. umbrinella*, which has smaller context hyphae (2–3 μ in diam.) and paler spores. Externally it is exactly like *Fomes johnsonianus*, but internally it differs in lacking setae and in having distinctly larger spores.

100. PORIA FLAVOMARGINATA (Murr.) Sacc. & Trott. Spores 2.5–3 × 2–2.5 μ, some becoming pale brown; setae occasionally present, 16–24 × 4–7 μ. On angiosperms in La. according to Baxter.

V. *GANODERMA* Karst. emend. Pat.

1a. Sporophores perennial; context dark purplish or reddish brown; upper surface usually dull

1. GANODERMA APPLANATUM (Pers. ex Wallr.) Pat. Crust on upper surface hard, not easily broken. On living and dead angiosperms throughout.

2. GANODERMA LOBATUM (Schw.) Atk. Upper crust thin and easily broken. On angiosperms in Md., D. C., W. Va., Va., N. C., Ga., Fla., Miss., Tenn., Ky., Ark., and La.

1b. Sporophores annual; context pale brownish to almost white; upper surface usually appearing varnished

3. GANODERMA LUCIDUM (Leys. ex Fries) Karst. Sporophore stipitate or sessile; spores 10–12 × 6–9 μ. On living angiosperms and also on stumps in Md., D. C., W. Va., Va., Ga. Fla., Ala., Miss., Tenn., Ky., Ark., and La. Var. *zonatus* (Murr.) Overh. has narrower spores and a strongly furrowed pileus. Syn.: *sulcatum* Murr.
4. GANODERMA TSUGAE Murr. Sporophore stipitate or sessile; spores 9–11 × 6–8 μ. On gymnosperms in W. Va., Va., N. C. and Tenn.
5. GANODERMA CURTISII Murr. Sporophores stipitate; spores 9–11 × 5–7 μ; upper surface bright ochraceus when young. On angiosperms in Md., W. Va., Va., N. C., S. C., Ga., Fla., Ala., Miss., Tenn., Ky., Ark., and La.
6. GANODERMA SUBTUBERCULOSUM Murr. Spores 10–12 × 7–8 μ. Known only from the type collection on Casuarina in Fla.

VI. *DAEDALEA* Fries

1a. Context tissue dark brown

1. DAEDALEA FARINACEA (Fries) Overh. Pore surface greenish; spores cylindrical, often curved, 5–8 × 2–3 μ. On angiosperms in D. C., W. Va., S. C., Fla., Ala., Tenn., and La. Syn.: *cinerascens* (Schw.), *coriaceus* (Berk. & Rav.).
2. DAEDALEA BERKELEYI Sacc. Pore surface brownish, often becoming lamellate; spores cylindrical, 7–8 × 2.5–3 μ. On gymnosperms in Va., S. C., Fla., Ala., Miss., Tenn., and La.

1b. Context tissue whitish to pale brown

2a. Pores very large, usually over 1 mm. in diameter

3. DAEDALEA JUNIPERINA Murr. Sporophores generally broadly effused and narrowly reflexed, or resupinate; becoming lamellate; spores cylindrical, 5.5–7 × 2.5–3 μ. On *Juniperus* in Md., D. C., Va., N. C., Fla., Miss., Ky., and Ark. Syn.: *westii* Murr.
4. DAEDALEA QUERCINA L. ex Fries. Sporophores usually sessile, applanate; becoming lamellate; spores cylindrical, 5–6 × 2–3 μ. On angiosperms, especially oak, in Md., D. C., W. Va., Va., and N. C.
5. DAEDALEA CONFRAGOSA Bolt. ex Fries. Sporophores sessile, applanate; often becoming lamellate; spores cylindrical, 7–9 × 2–2.5 μ; branched paraphyses in hymenium. On angiosperms in Md., D. C., W. Va., Va., N. C., S. C., Ga., Fla., Ala., Miss., Tenn., Ky., Ark., and La. Syn.: *albida* Schw., *zonata* Schw.

2b. Pores smaller, usually 2–4 per mm.

6. DAEDALEA UNICOLOR Bull. ex Fries. Upper surface often hirsute; context with thin black layers; spores ellipsoid, 5–6.5 × 3–3.5 μ. On angiosperms in Md., D. C., W. Va., Va., N. C., Tenn., and La.
7. DAEDALEA AMBIGUA Berk. Upper surface glabrous; spores cylindrical, 5–7 × 1.5–2.5 μ. On angiosperms in W. Va., N. C., S. C., Ga., Fla., Ala., Miss., Tenn., Ky., Ark., and La. Syn.: *Aesculi* (Fries), *Aesculi-flavae* (Schw.).

VII. *LENZITES* Fries

1a. Context tissue white to cream

1. LENZITES BETULINA (L. ex Fries) Fries. Spores cylindrical, 4–7 × 1.5–3 μ; cystidia present. On angiosperms in Md., D. C., W. Va., Va., N. C., S. C., Ga., Fla., Ala., Miss., Tenn., Ky., and Ark.

1b. Context tissue pale to dark brown

2. LENZITES SAEPIARIA (Wulf. ex Fries) Fries. Spores cylindrical, 8–10 × 3–3.5 μ. On gymnosperms, occasionally on angiosperms, in Md., W. Va., Va., N. C., S. C., Ga., Fla., Ala., Miss., Tenn., Ark., and La.
3. LENZITES TRABEA Pers. ex Fries. Spores cylindrical, 7.5–9 × 2.5–4 μ; often poroid. On angiosperms and wood in service in Md., W. Va., Va., N. C., S. C., Ga., Ala., Miss., Tenn., Ky., Ark., and La. Syn.: *vialis* Peck.
4. LENZITES STRIATA (Swartz ex Fries) Fries. Spores cylindrical to ellipsoid, 6–8 × 2–4 μ; cystidia abundant. On angiosperms in N. C., Ga., and Fla.

VIII. *FAVOLUS* Beauv. emend. Fries

1a. Spores ellipsoid to subglobose, less than 5 μ long; pores 3–4 per mm.

1. FAVOLUS RHIPIDIUM (Berk.) Sacc. Sporophore white when fresh, becoming reddish or pinkish on drying. On angiosperms in Va., S. C., Ga., Fla., Ala., Tenn., Ky., Ark., and La.

1b. Spores cylindrical to cylindric-ellipsoid; more than 5 μ long; pores 2 or less per mm.

2a. Pileus pubescent

2. FAVOLUS FLORIDANUS (Murr.) Sacc. & D. Sacc. Similar to *F. brasiliensis* except pileus not glabrous. Known only from the type collection on angiosperms in Fla.
3. FAVOLUS RENIFORMIS (Murr.) Sacc. & Trott. Hyphal pegs visible with hand lens; upper

surface often checkered. On angiosperms in Fla.

2b. Pileus glabrous

3a. Spores 14–20 μ long

4. FAVOLUS CUCULLATUS Mont. Stipe poorly developed; large hyphal pegs present. On angiosperms in Ga. and Fla. Syn.: *taxodii* (Murr.).

3b. Spores 8–11 μ long

5. FAVOLUS ALVEOLARIS (DC. ex Fries) Quél. Reddish at first, weathering to white or cream; stipe poorly developed. On angiosperms in Md., D. C., W. Va., Va., N. C., Ga., Ala., Tenn., and Ark. Syn.: *striatulus* Ell. & Everh.
6. FAVOLUS BRASILIENSIS Fries. Stipe distinct to poorly developed; sporophores white when fresh, drying to cream or pale tan. On angiosperms in Fla., and La. Syn.: *caespitosus* Lloyd.

IX. *HEXAGONA* Pollini emend. Fries

1. HEXAGONA VARIEGATA Berk. Sporophore very thin, sessile, dark brown above; context light brown. On angiosperms in Fla.

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The treatment of the genera *Poria* and *Fomes* and of the sessile species of *Polyporus* was prepared by Lowe, the other groups by Gilbertson; however responsibility is jointly shared by the authors.

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North Carolina Earthquakes, 1958 and 1959, with Additions and Corrections to Previous Lists

GERALD R. MACCARTHY
Department of Geology and Geography, University of North Carolina, Chapel Hill, N. C.

Recent Earthquakes

1958 During 1958 only one earthquake was definitely recorded from North Carolina; this occurred on March 5 at about 6:45 a.m. and was felt only in the general Wilmington area. At first glance it appeared to be another of a rather protracted series of tremors in that area which started about February 10 and continued for more than a month. Between February 10 and March 15, tremors were noticed on at least thirteen different days, some days having more than one. The majority of these occurred between 9:00 and 10:00 a.m. Because of this regularity in occurrence and certain other characteristics, they are thought to have been of an artificial origin, although no definite proof of this has been established.

Of the entire series, apparently only the one which occurred at about 6:45 a.m. on March 5 has been recorded on any seismograph. This one was recorded at Chapel Hill, N. C., and at Columbia, S. C., the Chapel Hill record being a regular textbook example of what a seismogram from a small, local earthquake should look like. Whatever the origin of the other tremors may have been, there seems little doubt that this one was a small genuine earthquake with its epicenter not far from Wilmington, probably off the coast. A few people in the Wilmington-Southport-Kure Beach area were somewhat alarmed by it, but no damage was reported. This occurrence has been described in some detail in *Earthquake Notes* (MacCarthy, 1958).

1959 During 1959 no earthquakes with epicenters in North Carolina were reported. However, on October 26, at about 9:10 p.m., a shock of very moderate intensity occurred in South Carolina and also shook up portions of Scotland, Richmond, Anson, and (probably) Union counties in North Carolina. The epicenter apparently was close to McBee, Chesterfield County, S. C. It was felt throughout an elliptical area oriented SW–NE, which extended from Columbia, S. C., to Hamlet and Rockingham, N. C., and, NW–SE, from Great Falls to Elliott in South Carolina. About 4000 square miles were affected. The greatest intensity noted did not exceed 4½ on the Modified Mercalli Scale. No damage was reported anywhere, and in North Carolina very little alarm was caused. This tremor was recorded on the seismograph at Chapel Hill at $9^h\ 7^m\ 59\frac{1}{2}^s$ p.m., eastern standard time. North Carolina communities which reported feeling this shock include: Lilesville, McFarlan, and Morven in Anson County; Cordova, Rockingham and Hamlet in Richmond County; Red Springs (doubtful) in Robeson County; and Laurel Hill and Gibson in Scotland County.

Additions and Corrections to Previous Lists

In two previous papers (MacCarthy, 1957; MacCarthy and Sinha, 1958) the writer has attempted to summarize the seismic history of North Carolina. Since these papers were published, enough additional information has come to light to warrant a third list, which is given below. This new listing adds eleven more earthquakes to the North Carolina tabulation, gives additional information concerning one previously listed, and deletes one from the record.

1808 December 13: about 5:30 a.m.: Raleigh. "On Tuesday Morning, about one and a half hours before day, this city experienced a slight earthquake. Previous to the shock a rumbling noise was heard, resembling very distant thunder." *Minerva* (Raleigh), Dec. 15, 1808.

1817 January 8: 4:00–5:00 a.m. The shock in the "fourth or fifth hour" of the morning, mentioned in a previous list (MacCarthy, 1957, p. 87), as having been felt in the Salem, N. C.,

area, was also felt over much of South Carolina and Georgia. Additional localities mentioned in contemporary accounts are: Charleston, S. C., New Bern, N. C., and Milledgeville, Ga. In the latter town the shock was so severe as to cause the bell in the State House to ring. The epicenter appears to have been quite close to Charleston, S. C. This earthquake is mentioned in the *Connecticut Courant*, Feb. 4, 1817; in the *National Intelligencer*, Jan. 16, 1817; and in the *Weekly Recorder* (Chillicothe, Ohio), Jan. 29, 1817.

1827 May 11: Wilkesboro. "We learn ... that a pretty severe shock of an Earthquake was felt at Wilkesborough (in this State) on Friday, the 11th inst. The doors and windows of the houses were sensibly shaken; and the water in the river was seen to have a tremulous motion. Something of a shock was felt at Wilkesborough, a year or two ago." *Star* (Raleigh), May 31, 1827. No other reference to this shock has been found.

1850 March 30: 10:00–11:00 a.m.: Wayne County. This shock seems to have been reported only from Wayne County. It was strong enough at Goldsboro to "cause certain pieces of furniture to rock in their places." Mentioned in the *Carolina Watchman* (Salisbury), Apr. 16, 1850, and in the *Raleigh Register*, Apr. 10, 1850.

1851 August 10: 8:55 p.m.: Asheville. "On Sunday evening last at 5 minutes before 9, a severe shock of earthquake was felt in this place, accompanied by a loud noise, which lasted 20 seconds.... We were sensibly moved in our chair, our house jarred, and many things in it moved so as to cause considerable noise." *Asheville Messenger*, quoted in the *Carolina Watchman*, Aug. 21, 1851.

1860 January 19: 6:00 or 7:00 p.m. (Times given differ in various accounts). This quake was felt in North Carolina, South Carolina, and Georgia, and reported from Charleston and Columbia in South Carolina; Augusta, Macon, and Atlanta in Georgia; and Wilmington (slight) in North Carolina. It was generally mentioned in contemporary newspapers, *e.g.*, the *Wilmington (Weekly) Journal*, Jan. 21, 1860, and the *National Intelligencer*, Jan. 21, 24, and 25, 1860. Despite the rather large area which was affected, this shock is not listed in *Earthquake History*.

1871 April 16: 12:00–1:00 a.m.: Wilmington. "Our city was visited with a very perceptible shock of an earthquake, on last Sunday morning, between 12 and 1 o'clock, the jarring being so great as in many instances to cause persons to jump up out of bed in alarm." *Wilmington Daily Journal*, Apr. 10, 1871.

1871 April 20: 9:00 p.m.: Oxford. "We learn by private letter that a slight shock of an earthquake was felt at Oxford, on Thursday night last, about 9 o'clock, p.m." *Telegram* (Raleigh), Apr. 27, 1871.

1877 October 8 (?): 8:00 p.m. Brevard and Hendersonville. A news item in the *New York Times*, Nov. 9, 1877, quoted from the *Charleston News* "of the 15th inst.", reports that an earthquake occurred at this time in the "Brexard-Henderson (*sic*)" area, which lasted "for several minutes" and which "frightened the inhabitants out of their wits." Reportedly it was not felt at Spartansburg or at Greenville, nor indeed "anywhere south of the mountains." Since no other reference to this supposed earthquake has been located, the above account may well be nothing other than a traveler's "tall tale."

1888 January 12: 9:54 a.m. Another Georgia-South Carolina-North Carolina shock. Reported in various contemporary newspapers as having shaken up Charlotte, Raleigh, Wilmington, Lenoir, Shelby, Fayetteville, etc. in North Carolina; Charles, Summerville, Georgetown, Conway, Beaufort, Newberry, and Columbia in South Carolina; and Augusta and Savannah in Georgia. The epicenter was apparently very close to Charleston, S. C., and, while the shock was quite severe in that area, no damage seems to have been reported anywhere. This rather extensive earthquake does not appear in *Earthquake History*.

1893 June 20: 11:05–11:20 a.m. Still another Carolina-Georgia earthquake. In North Carolina it was reported from Charlotte, Raleigh, Washington, Wilmington, Southport, New Bern, Mt. Pleasant, and Pittsboro. In South Carolina it was felt from Charleston to Columbia; in Georgia, Savannah, Augusta, and Brunswick reported it. In Wilmington, many people were awakened, but there seems to have been no damage anywhere. The epicenter was probably in South Carolina. Generally reported in the state newspapers. Not mentioned in *Earthquake History*.

1895 October 6: 11:30 p.m. Edgecombe County. Reported as being felt "nearly all over the county," but was not noted in Williamston, Rocky Mount, Wilson, or Greenville. Was felt in Tar-

boro and at Falkland. "Tarboro, N. C., Oct. 7, 1895.—Yesterday morning at 11:30 this community was startled by an earthquake shock. It first came [as a] noise as the distant firing of artillery, then came a wave motion that made the crockery and lamps rattle. . . . It frightened the people very much. . . ." *News and Observer* (Raleigh), Oct. 8, 1895.

1918 April 19: This shock, previously listed (MacCarthy, 1957) as having been felt at Roanoke City, N. C., should be deleted from the North Carolina tabulation. Tracing the original reference reveals that instead of Roanoke City, N. C.," the cite read "Roanoke, Va." —a much more probable locality.

Summary

During 1958 only one earthquake occurred within the boundaries of North Carolina. In 1959 there were none, although a South Carolina tremor on October 26 was felt in three or four North Carolina counties. Eleven nineteenth-century shocks are added to the state list and one, that of April 9, 1918, is deleted.

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Screening Tests of Hydrazides, Pyridazine Derivatives, and Related Compounds for Possible Influences on Plant Growth and Development[1]

VICTOR A. GREULACH
Department of Botany, University of North Carolina, Chapel Hill, N. C.

Although it has now been ten years since the marked inhibition of plant growth by maleic hydrazide (6-hydroxy-3(2H)-pyridazinone) was first announced by Schoene and Hoffman (1949), there have been no reports of comparable influences on plant growth and development by other pyridazine derivatives, other hydrazides, or related compounds. Greulach (1953) reported significant growth inhibition by succinic hydrazide, phenylhydrazine, HCl, isonicotinic hydrazide (rimifon), and 1-isonicotynyl-2-isopropyl hydrazide (marsilid), but in no case was the inhibition similar to that produced by MH. Offe (1953) found that acethydrazide inhibited plant growth but that a variety of other hydrazides, including phthalic acid hydrazide, were ineffective, as were several different amides. Loveless (1952) studied the influence of MH and of some of its components, derivatives, and analogues on the production of chromosome abnormalities in *Vicia*. Of these, only 3-pyridazinone showed activity comparable with that of MH, but at a much lower level. Loveless concluded that the slight observed activity may have been due to oxidation of some of the 3-pyridazinone to MH, since the 6-methyl derivative which could not be oxidized was inactive. Other inactive compounds included diformyl hydrazine, diacetyl hydrazine, and 2-pyridone. Succinic hydrazide, citraconic hydrazide (5-methyl maleic hydrazide), and 5-bromo-maleic hydrazide produced effects similar to MH but only at much higher concentrations, while 2,6-pyrimidine-diol and 2,3-pyrazine-diol were inactive. Loveless concludes that no modification of MH is possible without considerable or total loss of activity, and suggests that the slight activity of some compounds may result from their partial conversion to MH. Loveless was, of course, considering influence on chromosome abnormalities rather than on growth. Of the many compounds screened for their influence on plant growth by the Chemical-Biological Coordination Center of the National Academy of Sciences-National Research Council in cooperation with the Bureau of Plant Industry, U.S.D.A., and other agencies, only a few have been hydrazides, pyridazine derivatives, imides, or other compounds with similarities to MH. Of these, most have either been inactive, have had variable effects on different species, or have inhibited growth to a lesser degree than or in a different way from MH. Crotonhydrazide, for example, had little or no effect on sunflower, cucumber, or barley, although it inhibited beans 22 per cent and corn 21 per cent. N-methyl maleimide completely inhibited the growth of cucumber and sunflower and killed the tissues at the point of application.

The screening program reported on here was initiated in the belief that a more systematic survey of the influences of compounds with structural similarities to MH on plant growth might uncover compounds with effects comparable with MH and might also clarify the structural features of the MH molecule essential for the growth-inhibiting properties of the compound. Among the components and fragments of the MH molecule considered worth while testing were

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hydrazine, maleic acid, diformyl hydrazine, diacetyl hydrazine, acetamide, and maleamide. The analogues and derivatives included succinic hydrazide, citraconic (6-methyl maleic) hydrazide, chloromaleic hydrazide, o-phthalic hydrazide, monohydroxy maleic hydrazide, and dihydroxy maleic hydrazide. In addition to these cyclic hydrazides, it appeared worth while to investigate a variety of pyridazine derivatives, maleimide and other imides, and some noncyclic acid hydrazides.

Procedures and Methods

The initial problem of securing the desired compounds was difficult and time consuming, since many of the compounds were not available commercially and in several instances had never been synthesized. Dr. Lowell V. Heisey of the Department of Chemistry at Bridgewater College synthesized sixteen compounds especially for this study, the Southern Research Institute provided three, and chemical companies donated sixteen (Olin Matheson, 9; Wyandotte Chemicals, 5; Naugatuck Chemical, 1; and American Cyanamid, 1). The remainder of the fifty-three compounds were obtained from commercial sources. The sources of specific compounds are listed in Table I. Four of the compounds (3,6-dimethyldihydropyridazine, adipic hydrazide, quinoline hydrazide, and tartaric hydrazide) proved to be insoluble and were not used in the testing program. Three other compounds were insoluble in water but soluble in 2% sodium bicarbonate (4-pyridazineacetic acid, 3-aminophthalhydrazide, and o-phthalic hydrazide), while n-n-amyl succinimide was soluble in 2% ethanol. The controls for these tests were treated with the solvent solutions. The final list of forty-nine test compounds included all but a few of those desired, and in addition a number of compounds of secondary interest were included because of their availability.

All forty-nine compounds were tested on beans (*Phaseolus vulgaris*, var. Black Valentine), tomatoes (*Lycopersicum esculentum*, var. Southland), and germinating cucumber seeds (*Cucumis sativus*, var. National Pickling). The first three test procedures described below are modifications of those employed in the plant-growth-regulator screening program of the Chemical-Biological Coordination Center (1955).

Bean-a Test. Twenty-five mg. of the test compound were dissolved in 0.5 ml. of Tween 20 and then mixed well with 2 g. melted lanolin, approximately 12 mg. of the mixture being applied with the broad end of a toothpick as a smooth band about 7 mm. wide around the center of the first internodes of ten 7-day-old bean plants. The controls were treated with a Tween-lanolin mixture. The height of the stems from the cotyledons to the terminal buds was measured at treatment and 7 and 14 days after treatment, the plants being observed for injury and morphogenic effects.

Bean-b Test. Bean plants 14 days old were dipped in 0.01 molar solutions of the test compounds, ten plants per treatment. (This is a concentration at which maleic hydrazide is very effective.) The height of the plants was measured at treatment and 7 and 14 days after treatment, and the plants were checked for formative effects.

Germinating Cucumber Seed Test. To twenty-five cucumber seeds on filter paper in a petri dish 15 ml. of a 100 ppm. solution of the test compound were added. The dishes were covered and incubated at 28°C for 96 hours, when the length of the primary roots was measured. The controls were similarly supplied with water and all tests run in triplicate.

Tomato Test. Tomato plants seven weeks old were dipped in 0.01 molar solutions of the test compounds, ten plants per treatment. Measurements of stem height above the cotyledons were made at treatment and at weekly intervals for three weeks, at which time fresh- and dry-weight determinations of the shoots were made. The plants were observed for injury and formative effects at each measurement period. The tests were conducted in duplicate for most of the compounds.

All tests were analyzed for statistical significance by use of the *t* test, except where the means were so near those of the controls as to make lack of significance obvious. For purposes of tabulation the growth of the treated plants was calculated as per cent of the growth of the controls.

Results

Of the 48 compounds tested 21 inhibited growth significantly in one or more of the tests (Table I), data on these 21 being given in Table II. Although in a number of tests the mean height of the treated plants was greater than that of the controls, the increase was statistically significant only with n-bromosuccinimide in the bean-a test, where the growth of the treated plants was 168 per cent that of the controls.

Table 1

List of compounds tested, with sources and influence on plant growth.

No.	Compound	Source	Effect
	Pyridazines and Derivatives		
1.1	pyridazine		
1.2	3,6-dichloropyridazine		I
1.3	2(2,4-dinitrophenyl)-3,6-dimethylhydropyridazine	OM	
1.4	4-pyridazineacetic acid	SR	S
1.5	2,3-pyridazinecarboxylic acid		S
	Cyclic Hydrazides		
2.1	chloromaleic hydrazide	LH	I, S
2.2	methylitaconic hydrazide	LH	I
2.3	methylmaleic hydrazide	LH	I
2.4	o-phthalic hydrazide	OM	I, S
2.5	succinic hydrazide	LH	I
2.6	maleic hydrazide	NC	I, S
	Acid Hydrazides		
3.1	acethydrazide	LH	S
3.2	acetphenylhydrazide		I, S
3.3	3-aminophthalhydrazide		I, S
3.4	benzhydrazide		S
3.5	butyrlyl hydrazide	OM	I
3.6	maleic monohydrazide	LH	I
3.7	m-nitrobenzhydrazide		I, S
3.8	p-nitrobenzhydrazide		S
3.9	diacetyl hydrazide	OM	S
3.10	diformyl hydrazide	OM	I, S
3.11	difumaryl hydrazide	OM	I, S
3.12	itaconic dihydrazide	LH	I
3.13	maleic dihydrazide	LH	
3.14	oxalyl dihydrazide	SR	S
3.15	succinic dihydrazide	LH	I, S
4.1	hydrazine	OM	I
	Imides		
5.1	citraconimide	LH	
5.2	itaconimide	LH	
5.3	maleimide	LH	I, S
5.4	N-ethylmaleimide		I, S
5.5	methylmaleimide		I, S
5.6	phthalimide		S
5.7	N-(2-bromethyl) phthalimide		S
5.8	succinimide		
5.9	N-n-amylsuccinimide		I, S
5.10	N-bromosuccinimide		S
	Amides		
6.1	acetamide	AC	
6.2	acrylamide	AC	
6.3	fumaramide	LH	
6.4	maleamide	LH	I
6.5	succinamide	LH	
	Pyrazine and derivatives		
7.1	pyrazine		
7.2	pyrazine dicarboxylic acid		
7.3	2,5-dimethylpyrazine	WC	
7.4	2-methylpyrazine	WC	
	Piperazines		
8.1	2,5-dimethylpiperazine, cis	WC	S
8.2	2,5-dimethylpiperazine, trans	WC	
8.3	2-methylpiperazine	WC	

Notes on symbols: I—inhibited plant growth significantly in one or more test (see Table II); S—visible symptoms of injury or morphogenic effects (see Table II and text); LH—synthesized by Dr. Lowell V. Heisey, Department of Chemistry, Bridgewater College; AC—American Cyanamid Co.; NC—Naugatuck Chemical; OM—Olin Matheson Corp.; SR—Southern Research Institute, Birmingham; WC—Wyandotte Chemicals Corp. The remaining compounds were purchased from commercial sources.

Plant responses to most of the compounds were quite variable from species to species and between the bean plants treated with lanolin and solutions. Only succinic dihydrazide inhibited growth significantly in all four tests. Furthermore, there was extensive individual variation within most treatment groups, in contrast with the quite uniform responses of both beans and tomatoes to maleic hydrazide. As a result, the mean differences between the controls and treated plants were fre-

Table II

Data on compounds with significant growth-inhibiting influences in one or more tests, showing growth as per cent of the controls and visible symptoms of injury and morphogenic effects.

No.	Compound	Bean-a Test	Bean-b Test	Bean Symptoms	Tomato Test			Tomato Symptoms	Cucumber Test
					Height	Fresh weight	Dry weight		
1.2	3,6-dichloropyridazine	92	*87*		*82*	91	81		*74*
2.1	chloromaleic hydrazide	102	112	AbB	*79*	63	71		63
2.2	methylitaconic hydrazide	103	126		80	67	77		*57*
2.3	methylmaleic hydrazide	78	103		*67*	52	50		*74*
2.4	o-phthalic hydrazide	103	104	NtR	*59*	50	39		*67*
2.5	succinic hydrazide	128	104		*59*	57	68		*73*
2.6	maleic hydrazide	*35*	*23*	AbBMR	*30*	02	03	BMR	86
3.2	acetphenyl hydrazide	90	78	AblBCMNstMR	*48*	38	54	CNlR	79
3.3	3-aminophthal-hydrazide	119	138	AlNltR	*52*	45	49	M	94
3.5	butyrlyl hydrazide	94	96		*42*	33	60		96
3.6	maleic monohydrazide	80	112		*72*	54	69		93
3.7	m-nitrobenz-hydrazide	96	89	AblBNstR	*61*	40	44	Nst	*72*
3.10	diformyl hydrazide	*75*	97	AlCNs	*79*	67	61		90
3.11	difumaryl hydrazide	90	*82*		*70*	61	68	Nl	85
3.12	itaconic dihydrazide	100	*82*		90	85	100	Nt	*72*
3.15	succinic dihydrazide	*73*	*85*	Nt	*73*	68	57	Nt	*73*
4.1	hydrazine	95	107		*72*	59	48		82
5.3	maleimide	98	93	AlMNt	*04*	08	03	Nts	*74*
5.4	N-ethyl maleimide	111	76	AbBNst	*41*	50	28	MNst	80
5.5	methyl maleimide	125	*45*	AbNstR	*07*	14	03	MNlst	*76*
5.9	N-n-amyl succinimide	*64*	98	AbBlMNstR	81	91	56		74
6.4	maleamide	90	82		*73*	71	65		79

Notes: Bean-a test—lanolin, bean-b test—solutions. Bean and tomato data on stem growth, cucumber data on root growth. Key to symptom symbols: A—abscission; B—axillary buds developing; C—chlorosis; M—morphogenic effects on leaves; N—necrosis; R—reduced leaf area. b—buds; l—leaves; s—systemic effects; t—effects only on treated tissues. Italic data are statistically significant at the 1 per cent level. The tomato weights were not analyzed statistically.

quently quite large without being statistically significant. Growth inhibition in tomatoes was much more general than in beans, only seven compounds inhibiting bean growth significantly, though this may have been a result of differences in absorption rather than metabolic response. However, several of the compounds induced formative effects or injury in beans without inhibiting growth significantly.

Only maleimide and its derivatives inhibited growth to a degree characteristic of maleic hydrazide, but this marked growth inhibition was restricted to tomatoes, except for methyl maleimide in the bean-b (solution) test. Formative effects and injury were extensive with the maleimides and quite distinct from the formative effects of maleic hydrazide. In the bean-a (lanolin) test both methylmaleimide and n-ethylmaleimide consistently killed all cells at the point of application, producing a complete stem girdle. In all but a few plants, however, the girdle healed over by the growth of new tissue and both the roots and shoots continued to live.

The formative effects and symptoms of injury induced by the various compounds are summarized in Table II. Although growth inhibition was more extensive in tomatoes, visible symptoms were more common in beans. Nine different compounds caused bud or leaf abscission or both in beans while no abscission was observed in tomatoes. Maleic hydrazide induces terminal-bud abscission in bean plants, but other than this none of the formative effects or symptoms of injury induced by the compounds were comparable with those produced by MH. A number of the compounds caused necrosis at the point of treatment

or elsewhere (Table II) in both beans and tomatoes. Eleven of the compounds that did not inhibit stem growth caused injury or morphogenic effects (Table I), but these were of the same general types as those outlined in Table II and do not appear to be of sufficient general interest to warrant description and discussion. None of the compounds induced epinasty or had any morphogenic effects on stems, and the morphogenic effects on leaves consisted principally of minor changes in leaf shape and the crinkling and rolling of leaves.

Most of the compounds that inhibited stem growth in tomatoes caused an even more marked reduction in both fresh and dry weight. Since the weights of the shoots were taken by treatment groups rather than individual plants, the data were not susceptible to statistical treatment.

In view of the rather marked general difference in response of roots and stems to growth substances in general as well as of species differences in response, the effects of the various substances on cucumber-seedling root growth would not necessarily be expected to correlate closely with the tomato and bean stem growth responses. The cucumber test was also used for maleic hydrazide. Though the MH-treated plants grew only 86 per cent as much as the controls, the reduction was not statistically significant.

Considering the test compounds by classes (Table I), it may be noted that 3,6-dichloropyridazine was the only compound in the pyridazine group that significantly inhibited growth in any test, that all cyclic hydrazides inhibited growth in one or more test even though the growth inhibition was both quantitatively and qualitatively different from that induced by maleic hydrazide, that most of the acid hydrazides inhibited growth to some degree, that except for the maleimides and n-n-amylsuccinimide the imides were inactive, and that except for maleamide the amides, pyrazines, and piperazines were inactive.

Discussion

Except perhaps for the maleimides the compounds tested proved to be uniformly uninteresting and lacking in promise for either theoretical investigation or practical application. Although twenty-one of the compounds inhibited growth in one or more of the four tests, inhibition was variable from test to test and was generally much less marked than with a comparable concentration of MH; furthermore formative effects were

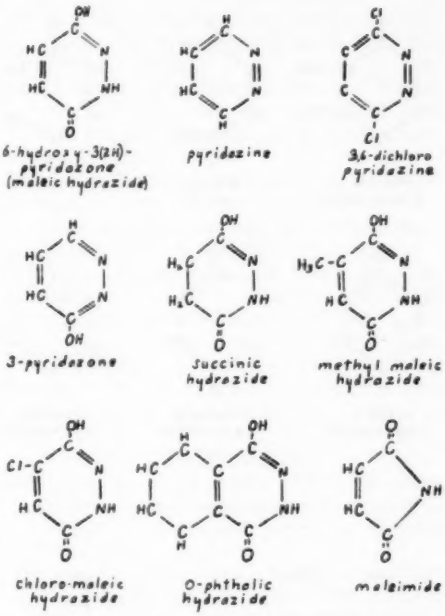

FIG. 1. Formulae of several compounds with structural similarities to maleic hydrazide. Of these, only maleimide and some of its derivatives inhibited growth to a degree comparable with maleic hydrazide, but the plant responses were quite different. Pyridazine had no detectable influence on plant growth. The other compounds inhibited growth, but to a much lesser extent than maleic hydrazide, and when formative effects occurred they were generally not typical of maleic hydrazide.

not similar to those produced by MH. While further investigation is needed to remove all doubt, the present data seem to justify the conclusion that none of the compounds tested have effects on growth comparable with those of maleic hydrazide. Since MH exerts its characteristic influences on plant growth at half the 0.01 molar concentrations used in this study, testing the compounds at a still higher concentration would not appear to be worth while. The data appear to justify a conclusion similar to that reached by Loveless (1952) in regard to the influence of related compounds on chromosome modifications: that any change from the MH molecule results in extensive, if not complete, loss of typical MH activity.

Considering only the compounds most similar to MH (Fig. 1), loss of the double bond between

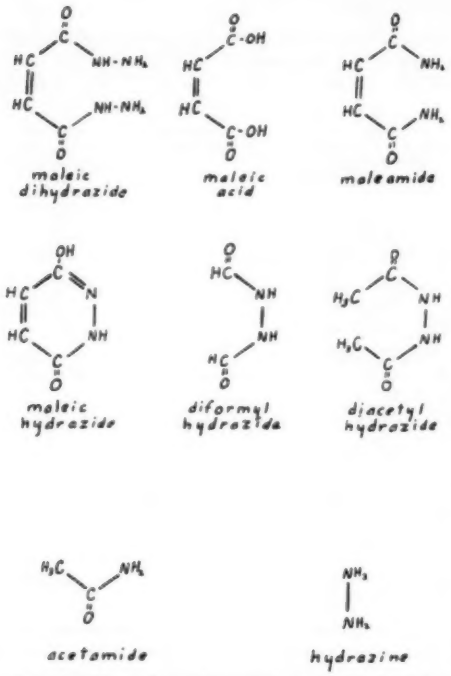

FIG. 2. Formulae of several compounds that have structural features of portions of the maleic hydrazide molecule, oriented to emphasize the similarities. Of these, maleamide and diformyl hydrazide inhibited growth significantly in one or more tests, but the degree and character of growth inhibition were not similar to that produced by maleic hydrazide.

carbons 4 and 5, as in succinic hydrazide, results in loss of typical MH activity though not in all influence on plant growth. This may also be a factor in the lack of typical MH activity in pyridazine and 3,6-dichloropyridazine. On the other hand, Loveless found that 3-pyridazinone (not available for the present tests) with HC=CH in the 4–5 position had some MH activity. Also, any substitution on the 4 or 5 carbons as in methylmaleic hydrazide, chloromaleic hydrazide, and o-phthalic hydrazide seems to result in loss of typical MH activity even though the double bond remains intact. At least one other factor should be considered in comparing MH with other cyclic hydrazides: Smith and Stone (1954) and Miller and White (1956) found that maleic hydrazide is 6-hydroxy-3(2H) pyridazinone (Fig. 1) rather than 3,6-pyridazine-dione, 1,2-dihydro as was formerly believed. If the other cyclic hydrazides have the 1,2-dihydro structure rather than the 6-hydroxy structure of MH, this may be a factor in the differences of their activity.

It may also be noted that maleimide and maleamide, both with a HC=CH group like that of MH, show much greater activity than other imides and amides. Unlike other compounds tested, maleimide and its derivatives have in the past been shown to have considerable biological activity. For example, Friedmann and others (1949) found that n-ethyl maleimide, methyl maleimide, and maleimide were active in inhibiting mitosis in chick fibroblasts. This is of particular interest since MH does not inhibit cell division in animals (Greulach et al., 1951; Barnes et al., 1957) as it does in plants (Greulach and Atchison, 1950; Darlington and McLeish, 1951), while maleimides are not definitely known to inhibit cell division in plants. However, the influence of maleimides on plant metabolism has been studied by several investigators including Van Overbeek et al. (1955), who found that n-phenyl and n-naphthyl and other maliemides act as antiauxins, inducing leaf abscission, inhibiting cell elongation, and reducing cold requirements for flowering. Maleimide growth inhibition of not more than 50 per cent could be reversed by auxins. Both Van Overbeek et al. and Friedmann et al. concluded that the maleimides were =SH poisons. Though several workers have suggested that maleic hydrazide might act as an =SH poison, Weller et al. (1957) secured experimental evidence to the contrary.

None of the compounds that may be regarded as fragments of the MH molecule (Fig. 2) inhibited growth in a manner quantitatively or qualitatively similar to MH inhibition, further strengthening the conclusion that any modification of the MH molecule results in extensive if not complete loss of typical MH activity. Of particular interest are maleamide, which differs from MH in lacking ring closure between the nitrogen atoms, and diacetyl hydrazide, which differs in lacking ring closure between the carbon atoms (4 and 5 in MH).

In a previous paper (Greulach, 1953) the writer pointed out that succinic hydrazide was essentially insoluble. It has subsequently been discovered that the compound supplied as succinic hydrazide was actually a polymer and that true succinic hydrazide prepared by the newer syn-

thetic method of Feuer et al. (1951) by the reduction of maleic hydrazide is freely soluble in water. The succinic hydrazide used in these tests was prepared by this method.

Summary

The influence of 48 hydrazides, imides, amides, and heterocyclic nitrogen compounds on the growth of bean plants (when applied in both solution and lanolin), tomato plants, and cucumber seedlings (solutions only) was investigated. Most of the hydrazides, maleimide and its methyl and n-ethyl derivatives, maleamide, and 3,6-dichlorophridazine, inhibited plant growth significantly in one or more of the tests, and 23 of the compounds induced visible symptoms of injury or morphogenic effects on either beans or tomatoes or both. Except perhaps for the maleimides, none of the compounds promises to be of either theoretical or practical interest as a growth regulator. Though applied in concentrations well above those required for typical maleic hydrazide responses, none of the compounds induced these typical maleic hydrazide responses even though some (such as succinic hydrazide, chloro-maleic hydrazide, and methyl-maleic hydrazide) differ from MH only in minor details. The tentative conclusion is drawn that any modification of the MH molecule results in loss of typical activity, though not necessarily of all growth-inhibiting action. A similar conclusion was reached by Loveless (1952) regarding the effects of compounds related to MH on chromosome modification.

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A Botanical Reconnaissance of Portsmouth Island, North Carolina

C. John Burk
Department of Botany, University of North Carolina, Chapel Hill, N. C.

The northern half of the North Carolina coast is separated from the mainland by a chain of barrier islands known as the Outer Banks. Descriptive floras of several of these islands exist in the literature (Brown, 1959; Johnson, 1900; Kearney, 1900; Lewis, 1917). No floristic treatment of Portsmouth Island is available, however, and since the author and Mr. P. J. Crutchfield noted several distinctive features of the vegetation of this island during a brief collecting trip to the island on August 8, 1959, he believes that a recounting of these features, in addition to a listing of the seventy-three species of vascular plants which were collected, might contribute a necessary link in the series of separate insular floras which are inevitably preliminary to a floristic interpretation of the Outer Banks as a physiographic province.

Portsmouth Island lies at the northern tip of Core Banks, directly south of Ocracoke Island, from which it is separated by an inlet several miles wide. Perhaps the most practical definition of the limits of the island itself is that it comprises the area including Portsmouth Village and its immediate environs; the portion of Core Banks from below the village south to Cape Lookout is interrupted at various points by inlets, is completely uninhabited, and comprises a distinct unit which awaits a separate treatment.

The recent history of Portsmouth Island is rather unusual and has had a sufficient effect on the flora to be worth recapitulating. During the eighteenth century, the main channel at Ocracoke Inlet lay on the south side, closer to Core Banks than to Ocracoke Island. Large vessels could enter the inlet and pass through the channel to "commodiously ride at anchor in the harbor adjoining Core Banks" (Stick, 1958). In 1753, the Colonial Assembly authorized the laying out of a town on the heretofore apparently uninhabited island to provide wharves, warehouses, and other facilities for these ships. The resultant town of Portsmouth was the first, and for many years the largest, settlement on the Outer Banks.

By 1800, the population had risen to 246 persons. In the next fifty years, it rose to a recorded high point of 505, while the village acquired an "academy," a post office, and a marine hospital constructed by the federal government. During this time, however, the harbor had begun to shoal up, and after the hurricane season of 1846, when both Hatteras and Oregon Inlets were opened, most of the trade which had previously come to Portsmouth approached the mainland through the newer inlets. From that time to the present, the population has dropped steadily until in 1950 there were only fourteen people living on the island, and in the summer of 1959, according to local report, there were just eleven, "none of them under seventy and no two of them married." A number of abandoned houses, the church, the post office, several outbuildings, and an abandoned coastguard station are still standing. The harbor itself has shoaled to the extent that the island must be approached in a small skiff.

Apparently human settlement on the Outer Banks, even before the advent of the white man (Haag, 1958), has always been in those places where the barrier islands are widest and the terrain is sufficiently protected from the ravages of the sea. These same sites, being ecologically less rigorous, are usually most advantageous to the development of a full vegetative physiognomy. Portsmouth Island, then, might be interpreted as an area in which the effects of man's encroachment on what was probably never a particularly stable biotic community were followed by a return, once physiographic changes made the land even less compatible with man's activities, to what was presumably the original vegetative pattern.

In the contrast to the more stable of the barrier islands on the Outer Banks, Portsmouth Island possesses only a vestige of a protective dune between the Atlantic Ocean and the vegetated portions of the island. About a quarter mile of flat moist sand, devoid of plant life, affords the only

protection from salt water and, equally important (Boyce, 1954), from airborne salt spray. This absence of an effective shield has resulted in a vegetative profile different from that of most of the barrier islands on the Banks.

Behind the sand flat, low hummocks support clumped dune grasses, primarily *Spartina patens* and *Uniola paniculata*. Several herbs, most of them succulents, occur in association with these grasses. They are *Cakile edentula*, *Croton punctatus*, *Euphorbia polygonifolia*, *Hypericum gentianoides*, and *Oenothera humifusa*. The stems, rhizomes, and peltate leaves of *Hydrocotyle bonariensis* appear to act as rather effective sand binders over some of these hummocks. Two shrubs, *Rubus trivialis* and *Iva imbricata*, as well as such vines as *Smilax bonanox* and *Parthenocissus quinquefolia* also occur in this area.

Behind these hummocks lie the remains of the village of Portsmouth. While the live oak, *Quercus virginiana*, is abundant on most of the islands which make up the Outer Banks, both as a dominant plant in the shrub zone and in the maritime forest (Bourdeaux and Oosting, 1959) and as the most common shade tree in the villages, no live oaks whatever were observed on Portsmouth Island. *Ilex vomitoria* and *Bumelia lycioides*, both common shrubs or small trees of the maritime forest, did occur in the village area, along with a few struggling specimens of *Pinus taeda*. *Ficus carica*, *Euonymus patens* Rehd., *Prunus angustifolia*, and *Populus alba* are three apparent cultigens which have survived abandonment about old home sites. Local inhabitants believe the fig, *Ficus*, to be native to the area. *Populus alba*, on Portsmouth as well as on other portions of the Banks, has escaped into the natural communities, being particularly abundant in the stands of red cedar.

This cedar, *Juniperus virginiana*, is the only tree of any real importance on the island. It occurs in small stands both within the salt marsh and within the environs of the village.

Gaillardia pulchella is a common ornamental which has escaped cultivation onto the dunes in the vicinity of the old coastguard station. This plant, in its two color forms, is quite common around most habitations on the Banks.

The salt marsh itself has intruded well into what was once Portsmouth Village, extending in most places as far seaward as the first dunelike hummocks except for strips of land where constantly maintained dikes have been erected for use as roadways, above the marsh, connecting those homesites which are still in use. The common salt-marsh shrubs—*Baccharis halimifolia*, *Iva frutescens*, and *Myrica cerifera*—grow to the very foundations of the abandoned houses. A few fresh-water pools support such herbs as *Lippia nodiflora*, *Bacopa monnieri*, and *Polygonum puncatum* about their edges, and the remainder of the island, to the edges of the sound, comprises a large and complex salt-marsh formation. *Juncus roemerianus* and *Spartina alterniflora* form the most extensive pure-species stands within this formation. In addition to them, a large number of salt-marsh herbs of varying ecological preferences occur in some abundance. These include *Ambrosia artemisiifolia*, *Atriplex patula*, *Borrichia frutescens* (a slightly woody composite), *Cyperus odoratus*, *C. polystachyos* var. *texensis*, *C. retrorsus*, *C. strigosus*, *Distichlis spicata*, *Eleocharis albida*, *Fimbristylis autumnalis*, *F. spadicea*, *Gerardia maritima*, *Juncus biflorus*, *J. dichotomous*, *Kosteletzkya virginica*, *Pluchea purpurascens*, *Sabatia stellaris*, *Salicornia bigelovii*, and *S. virginica*.

Other species collected from a variety of sites include *Cenchrus pauciflorus*, *Commelina erecta*, *Cucurbita pepo*, *Desmodium paniculatum*, *Diodia virginiana*, *Elymus virginicus* var. *halophilus*, *Eragrostis refractus*, *Erechtites hieracifolia*, *Erigeron pusillus*, *Euphorbia supina*, *Gaura angustifolia* Michx., *Ipomoea sagittata*, *Juncus scirpoides*, *Lepidium virginicum*, *Paspalum distichum*, *P. laeve*, *Phytolacca americana*, *Polypremum procumbens*, *Ptilimnium capillaceum*, *Rumex crispus*, *R. hastatulus*, *Setaria geniculata*, *Solidago sempervirens*, and *Stenotaphrum secundatum*.

All nomenclature used in this paper follows Fernald (1950) except in those cases where the specific author has been included with the listing of the species. All specimens collected in the course of this study have been deposited in the herbarium of the University of North Carolina.

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Some Free-Living Marine Nematodes from the Sand Beaches of Piver's Island, North Carolina

JOHN L. CRITES
Department of Zoology and Entomology, Ohio State University, Columbus, Ohio

In the United States, with its 9,000 miles of coastline, only a few investigators have studied free-living marine nematodes. Cobb (1915, 1917, 1920, 1922, 1928, 1930, 1933) described many new forms; other investigators have been Steiner and Albin (1933), Chitwood (1935, 1936a, 1936b, 1937, 1951), Chitwood and Chitwood (1938), Chitwood and Timm (1954), Allgén (1947b), Timm (1951a, 1951b, 1952, 1953) and Wieser (1959). As these workers have pointed out, the vast number of species from this habitat has hardly been touched.

During the summer of 1958, I made extensive collections of marine nematodes in the vicinity of the Duke University Marine Biological Laboratory, Piver's Island, Beaufort, North Carolina. The study reported here covers only a very small portion of this material. The work was supported by the National Science Foundation through the Duke University Marine Laboratory. Only Chitwood (1935, 1936a, 1936b, 1937) has previously reported on marine nematodes from the coast of North Carolina.

The nematodes covered in this report are from a four-dram sample taken on June 17, 1958, from the beach on the east side of Piver's Island near the Duke University boat dock. The sample is from the upper three inches of sand and it was taken at the high-tide mark. The upper layers of sand are fine grained, have a low organic content, and are free from boulders and aquatic plants. The salinity of the sea water was 33‰.

The nematodes were removed from the sample, heated gently in sea water until all movement ceased, and fixed with AFA. The specimens were cleared by placing them in glycerine alcohol which was evaporated slowly to glycerine. For detailed study, the worms were mounted in pure glycerine and covered with a No. 1 cover slip supported by glass wool to avoid crushing the specimens. Most species of marine nematodes must be determined with the aid of an oil-immersion objective.

Specific determination requires certain measurements which are usually expressed as de Man ratio formulae:

$$a = \frac{\text{total body length}}{\text{maximum body width}}$$

$$b = \frac{\text{total body length}}{\text{length of esophagus}}$$

$$c = \frac{\text{total body length}}{\text{length of tail}}$$

I followed the taxonomy of Chitwood (1951) in this study. All measurements were made from specimens under supported cover slips and from specimens which were killed with mild heat. The following species were recovered.

CLASS APHASMIDIA

Order Chromadorida
Suborder Chromadorina
Superfamily Desmodoroidea Steiner, 1927
Family Desmodoridae Micol., 1924
Subfamily Richtersiinae Cobb, 1933

Neonyx Cobb, 1933

The genus Neonyx was proposed by Cobb; the type species is *N. cancellatus* Cobb, 1933. Other species in the genus are: *N. alatus* Cobb, 1933, sp. inq.; *N. camycoma* Cobb, 1933; *N. onyxoides* (Chitwood, 1936) and *N. obesus* (Chitwood, 1936).

Chitwood (1936) and Gerlach (1951a) synonymized the genus *Neonyx* with the genus *Metachromadora*. In 1952, Timm re-established the genus *Neonyx*. He pointed out that it differs from *Metachromadora* in the finer striation of the cuticle, in the absence of a nonrigid cephalic capsule marked with longitudinal striations, and in the double curvature of the stoma wall opposite the dorsal tooth.

Neonyx obesus (Chitwood, 1936)

Description: Cuticle striated. Prominent lateral alae. Stoma and esophageal lining heavily sclerotized. Anterior circle of six short cephalic setae, posterior circle of four longer setae. Somatic setae numerous. Amphids distinctly spiral. Esophagus somewhat expanded around stoma and greatly enlarged at base. Sclerotized lining dividing posterior expanded portion of esophagus into three regions.

Male: 0.79 to 0.86 mm. long; a, 16 to 21; b, 5.7 to 6.4; c, 8.2 to 9.7. Testes 24% of the body length from anterior end; large rounded spermatocytes 9 to 11 microns in width. Thick spicules; eight supplentary organs placed on conspicuously raised medioventral elevation.

Female: 0.87 to 0.92 mm. long; a, 10 to 14.4; b, 4.3 to 5; c, 10.3 to 12.2. Vulva 54.2 to 58.3%. Ovaries reflexed. Tail 3.3 to 3.5 anal diameters. Minute setae in subventral vulvular region.

Neonyx asupplementus, n. sp. (Figs. 1, 2, 3, 4, 5)

Description: Cuticle moderately striated, striations 13.5 microns apart. Lateral alae absent. Nonrigid cephalic helmet, without longitudinal striations. Oral opening ovoid; anterior circle of six short setae and posterior circle of four long ones. Subcephalic setae present, somewhat variable. Somatic setae rather numerous. Stoma moderately sclerotized, large dorsal tooth and curvatures opposite it heavily sclerotized. Amphids indistinctly spiraled, one-half width of head. Esophagus terminated by elongated swelling 0.45 length of esophagus, sclerotized lining divides swelling into three distinct regions.

Male: 1.2 to 1.3 mm. long; a, 33.5 to 37; b, 6.8 to 7.3; c, 17 to 19.5. Testes 33% of the body length from anterior end. Spicules arcuate and cephalated, 1.8 anal diameters or 54.6 to 59.2 microns long. Gubernaculum 0.55 the length of the spicule. Supplements absent.

Female: 1.15 to 1.27 mm. long; a, 27.9 to 31.9; b, 6.58 to 7.9; c, 16.29 to 18.59. Vulva 57% to 58% of body length from anterior end. Ovaries reflexed, $ovary_1$ 19 to 19.6% and $ovary_2$ 17.3 to 19.6% of body length. Oviparous; egg 87 to 94 microns long by 23 to 26 microns wide. Tail 1.76 to 2 anal diameters long.

Neonyx asupplementus may be distinguished from other forms as follows: *N. cancellatus* has eight longitudinal rows of five setae in the cephalic region; *N. alatus* Cobb, 1933, sp. inq. and *N. campycoma* have lateral alae; *N. obesus* has lateral alae and distinctly spiraled amphids, and the male has eight supplementary organs on a raised medioventral elevation; the female of *N. obesus* has a heavy coat of setae in the subventral vulvular region; *N. onyxoides* has nine to ten male supplementary organs on a slight medioventral elevation; the eggs of *N. onyxoides* are 74 by 41 microns while those of *N. asupplementus* are 87 to 94 microns long by 23 to 26 microns wide.

The males of *N. asupplementus* were examined in both lateral and ventral views, and no male supplementary organs could be found.

Superfamily Chromadoroidea Stekhoven and de Coninck, 1933

Family Chromadoridae Filipjev, 1917

Subfamily Chromadorinae Micoletsky, 1922

Allgéniella Strand, 1934

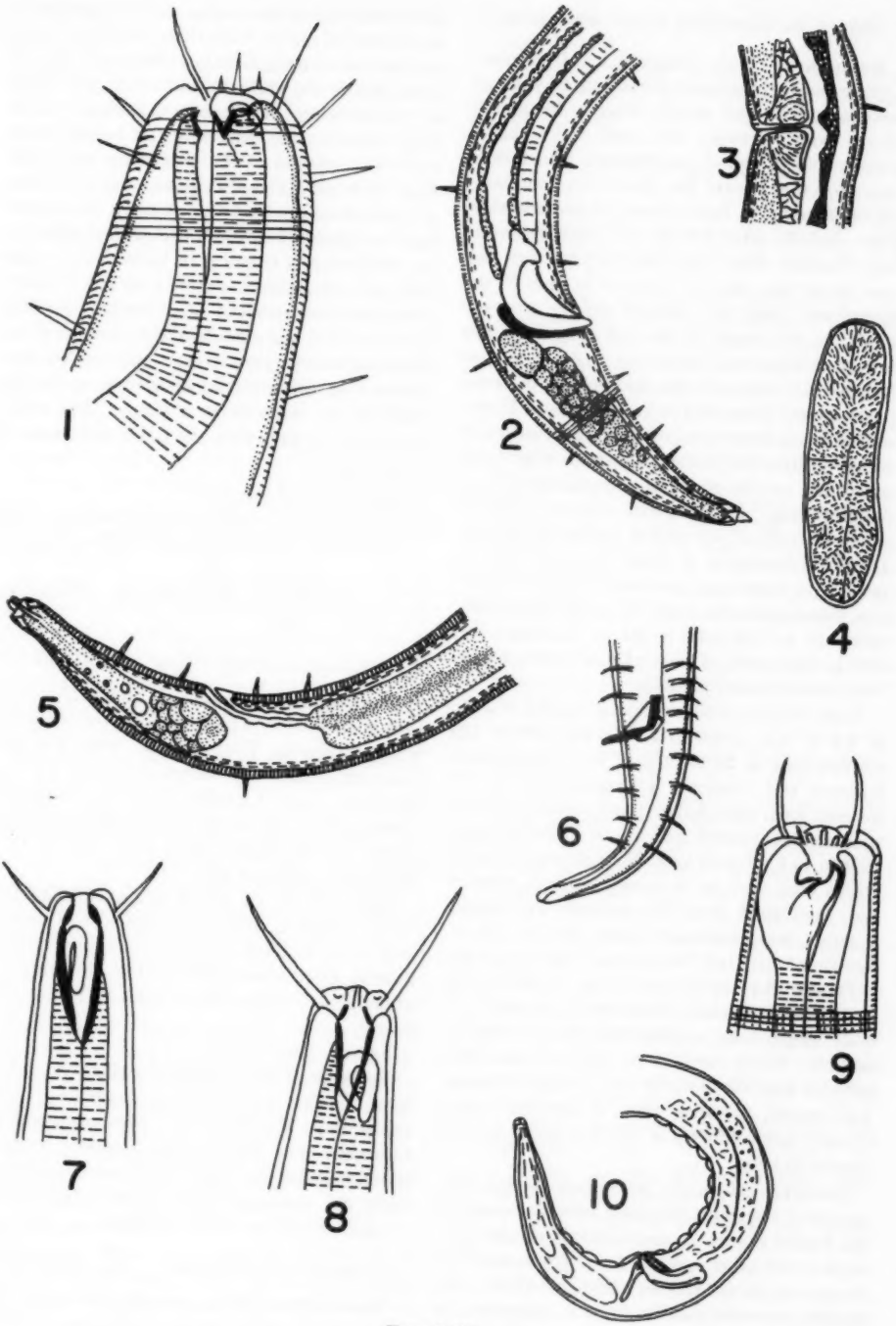
The name *Allgéniella* was first applied to this genus by Strand (1934). Filipjev (1930) had described the genus *Odontonema* for a new species *O. guido-schneideri*. He transferred *Spilophora trichophora* Steiner, 1921, *Chromadora tenuis* G. Schneider, 1926, and *Chromadora hyalocephala* Steiner, 1916, to the genus *Odontonema*. In 1934, Strand pointed out that the name *Odontonema* was preoccupied, having been used by Weber (1913) for a fish, and changed the name to *Allgéniella*. Allgén (1936) confirmed Filipjev's original work and the name change by Strand, but added little to the diagnosis of the genus. Schulz (1939) reported *A. trichophora* (Steiner), and Gerlach (1951b) reported *A. tenuis* (G. Schneider) from the coast of Germany.

FIGS. 1–5—*Neonyx asupplementus*. Fig. 1, anterior end, lateral view; Fig. 2, male tail, lateral view; Fig. 3, female vulvular region, lateral view; Fig. 4, ovum; Fig. 5, female tail, lateral view.

FIGS. 6 and 9—*Allgéniella macrodonta*. Fig. 6, male tail, lateral view; Fig. 9, anterior end, lateral view.

FIG. 7—*Axonolaimus steineri*, anterior end, lateral view.

FIGS. 8 and 10—*Axonolaimus stomomilivus*. Fig. 8, anterior end, lateral view; Fig. 10, male tail, lateral view.



FIGS. 1–10

Allgéniella macrodonta, n. sp. (Figs. 6, 9)

Description: Body fusiform. Tail conical. Cuticle distinctly striated. Striations 1.4 microns apart anteriorly and on tail, closer in the middle of the body. Between striations cuticle has a series of small round punctations. Punctations closer together toward the anterior end and lacking on lateral alae. Lateral alae 3.4 microns wide. Four cephalic setae 0.86 to 1.2 head diameters long. Somatic setae numerous, in four rows, one row dorsal and one row ventral to each of the lateral alae. Each row setae of somatic setae extends the full length of the body; setae shorter toward anterior end measuring 13.6 microns, as long as 27 microns in the middle and posterior parts of body. Stoma 6.8 to 8 microns deep. Dorsal wall of stoma is provided with large, curved tooth which projects into lumen. Dorsal to large tooth sclerotized crevice giving the appearance of one nonprojecting, second tooth. Dorsal wall of stoma sclerotized but ventral wall lacks sclerotization. Musculature of tooth produces marked swelling in dorsal and anterior section of esophagus. Esophagus terminated by conspicuous bulb, bulb 0.21 to 0.26 total length of esophagus and 0.78 to 0.85 width of body at base of esophagus. Very small spiraled amphids.

Male: 0.492 to 0.503 mm. long; a, 22.4 to 24.1; b, 5.2 to 5.7; c, 6.0 to 7.7. Testes 120 to 129 microns long or 24 to 26% of body length from anterior end. Spicules L-shaped, 27.8 to 29 microns long, uncephalated and accompanied by well defined ventral membrane. Gubernaculum 12.9 to 14.3 microns long. No male supplements. Nerve cord 52.4 to 54.4 microns from anterior end. Anal width 19 to 21.8 microns. Tail conoid, tapering, tube of spinneret opens dorsally just before tip of tail. Tail 3 to 3.9 anal diameters long.

Female: 0.41 to 0.5 mm. long; a, 20 to 24.5; b, 5 to 5.8; c, 5.6 to 6. Vulva 48.9% to 50.6% of body length from anterior end. Ovaries slightly reflexed. Nerve cord 51 to 54.4 microns from anterior end. Anal width 19.7 to 20.4 microns. Tail conoid, tapering, tube of spinneret opens dorsally just before tip of tail. Tail 3.2 to 3.6 anal diameters long.

Remarks: *Allgéniella macrodonta* is the only species of the genus described from the coasts of the United States. *A. macrodonta* is shorter than most of the other species of the genus, and it is closest to *A. pachydema* (Filipjev, 1930). *Allgéniella macrodonta* differs from *A. pachydema* in several respects. *A. pachydema* has a wider body; the dorsal wall of the esophagus of *A. pachydema* has a series of pleats, while there is only one in *A. macrodonta*; *A. pachydema* has a weakly developed esophageal bulb, while the bulb of *A. macrodonta* is well developed; *A. macrodonta* has four rows of long somatic setae extending the length of the body; the spicules of *A. macrodonta* vary from those of *A. pachydema* in size and shape; those of *A. pachydema* are curved, but in *A. macrodonta* they are almost L-shaped; the gubernaculum of *A. pachydema* is truncate in lateral view, while that of *A. macrodonta* is more slender; *A. pachydema* has seven or eight small pre-anal papillae. *A. macrodonta* was examined with both light and phase microscopes, and no pre-anal papillae were observed in either lateral or ventral views; the vagina of *A. macrondonta* is shorter, and tail of the female is longer than the tail of the female of *A. pachydema*.

Suborder Monhysterina
Superfamily Axonolaimoidea Chitwood, 1937
Family Axonolaimidae Stekhoven and de Coninck, 1933
Subfamily Axonolaiminae Micoletsky, 1924

Axonolaimus steineri Timm, 1952 (Fig. 7)

Description: Cuticle smooth. Stoma 23 microns long, more heavily sclerotized at anterior end but without odontia. Four cephalic setae 1.8 head diameters long. Four subcephalic setae 1.2 head diameters long. Amphids collapsed, shepherd's crook in shape, 10 microns long overlying anterior portion of esophagus. Nerve ring 7.9% of body length from anterior end.

Male: 1.58 to 1.7 mm. long; a, 53.25 to 57.3; b, 7.8 to 8.03; c, 10.5 to 11.8. Spicules 34 microns long or 1.3 to 1.4 anal diameters. Gubernaculum present. Long setae absent on tail. Tail conically attenuated with blunt tip, 5.4 anal body diameters long.

Female: Unknown.

Remarks: Timm (1952) described *A. steineri* from offshore sand at Sandy Point and Chesapeake Bay, Maryland. The specimens which I recovered from Piver's Island closely resemble those described by Timm with one minor exception: the specimens from Piver's Island have amphids which are more collapsed.

Axonolaimus stomamilivus, n. sp., (Figs. 8, 10)

Description: Cuticle smooth with only slight indication of striae at edges. Six lips, six labial

papillae and six cephalic papillae. Four cephalic setae, 1.6 head diameters long. Few scattered somatic setae. Stoma with sclerotized, tapering walls, kite or shield shaped in lateral view, 18.7 to 20.3 microns long. Amphids loop shaped, overlying posterior end of stoma and extending slightly beyond it posteriad. Esophagus swollen at base to about 0.75 body width. Excretory pore 2.2 to 2.5 stomal lengths from anterior end. Esophagus 11.2 to 12% of body length. Nerve ring 6.0 to 6.7% of body length from anterior end.

Male: 1.2 to 1.7 mm. long; a, 52.9 to 56.8; b, 7.8 to 8.6; c, 14.3 to 17.7. Spicules cephalated, 34 to 39 microns long or 1.3 to 1.6 anal body diameters. Gubernaculum with median piece projecting dorsoposteriad and small side piece. A row of 12 to 13 unicellular preanal glands. Tail 3.2 to 4 anal diameters long, tapering, and conically attenuated with blunt tip.

Female: 1.46 to 1.8 mm. long; a, 41.2 to 52.6; b, 7.0 to 8.3; c, 14.8 to 15.0. Vulva, 51.5%. $Ovary_1$ 21% and $Ovary_2$ 22% of the body length. Tail 3.9 anal diameters.

Remarks: *Axonolaimus stomamilivus* resembles *A. filipjevi* Timm, 1952, more closely than any other species described from the Atlantic coast of the United States. It varies from *A. filipjevi* in body ratios, in shape and depth of the stoma, and in position of the amphids. *A. stomamilivus* has a longer tail and longer setae.

In many respects this species resembles *A. longisetosus* Allgén, 1947, from Storfassen Island, Norway. It is closer to *A. longisetosus* than any other species in the genus in body ratios. However, *A. stomamilivus* differs from *A. longisetosus* in shape, size, and position of the amphids, in the length of the tail, and in the shape and depth of the stoma. Allgén describes no pre-anal glands in the male of *A. longisetosus*.

Odontophora sp.

Description: Cuticle smooth. Stoma heavily sclerotized, 18.7 microns long, V-shaped, with six odontia. Four cephalic setae, 0.8 head diameters long. Few scattered somatic setae. Amphids collapsed shepherd's crook in shape.

Juvenile: 1.2 mm. long; a, 49.6; b, 6.5; c, 9.7. Esophagus 15.4% of body length. Nerve ring 9.7% of body length from anterior end. Tail 5 anal diameters long.

Remarks: This worm, though similar to *O. axonolaimoides* Timm, 1952, has a longer stoma and longer cephalic setae. The body ratios are similar to those given by Timm (1952) for *O. axonolaimoides* except for the ratio of the tail to the body length.

Type specimens are deposited in Helminthological Collection of the Department of Zoology and Entomology, The Ohio State University.

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Three New Homalorhage Kinorhynchs from the San Juan Archipelago, Washington

ROBERT P. HIGGINS
Department of Zoology, Duke University, Durham, N. C.

The phylum Kinorhyncha (Echinodera) is often, and quite unjustly, referred to as one of the rare, lesser known invertebrate phyla. By no means should this group of microscopic marine "aschelminths" be considered rare; perhaps they should be considered rarely sought. Nearly all of our information on the Kinorhyncha comes from the monograph by Zelinka (1928). Remane (1936), Hyman (1951), and a few others have summarized the accumulated information on the phylum but very little original work has been carried out since 1928. Nyholm's (1947) study on postembryonic development and the phylogenetic discussion by Lang (1949) have been the only papers incorporating more than strictly taxonomic information, and even taxonomic papers on kinorhynchs have been uncommon.

Kinorhynchs are microscopic marine invertebrates which generally inhabit mud, sand, and algal substrates. Their size ranges from 50 μ in the case of certain larval stages (Nyholm, *l.c.*) to nearly one millimeter in length. The wormlike segmented body is feebly armored in the larval stages and is hyaline in appearance, whereas the adults develop a relatively thick exoskeleton which becomes yellow to yellow-brown in color. The head region is generally spherical when everted from the trunk and is provided with rings of posteriorly directed, curved spines; the posterior ring of these spines may be modified as sensory structures. A mouth cone, variously provided with small, anteriorly directed spines, protrudes from the anteriormost part of the head. The head is joined to the trunk by a short, variously plated neck, the neck plates being termed placids. The head and neck comprise the first and second zonites or body segments.

The trunk region shows a more distinctly segmented series of armored plates. The plate arrangement of the neck and first trunk zonites provide the primary basis for subdivision of the phylum into three suborders: Cyclorhagae, Conchorhagae, and Homalorhagae. The trunk region is generally flattened ventrally and arched dorsally, resulting in a triangular appearance in cross section. Spines are often located middorsally, laterally, and caudally on the trunk region. The shape and position of the various trunk spines provide the primary basis for further classification of the three suborders.

The scarcity of kinorhynch literature from North America has been discussed in a previous paper (Higgins, 1960). Homalorhage kinorhynchs have been reported from two regions in North America. Blake (1930) described *Pycnophyes frequens* and *Trachydemus mainensis* from Mount Desert Island, Maine; Wieser (1960) reported these same species from Buzzards Bay, Massachusetts; and Chitwood (1951) reported finding specimens of *Pycnophyes frequens* at Beaufort, North Carolina.

During the summer of 1958, I found a relatively large series of kinorhynchs while studying at the University of Washington Laboratories, Friday Harbor, Washington. In addition to seven specimens of *Echinoderes pennaki* Higgins (Higgins, 1960), a cyclorhage kinorhynch, I collected two specimens of a previously undescribed species of *Pycnophyes* as well as several hundred specimens of two undescribed species of *Trachydemus*. The latter two genera are both homalorhage kinorhynchs. The presence of lateral end spines in the genus *Pycnophyes* is the single character separating it from the genus *Trachydemus*.

The suborder Homalorhagae consists of a single family with two genera. The suborder is separated from the other two suborders on the basis of retractable placids and the division of the ventral plate of the third zonite (first trunk zonite) into three separate plates which constitute the "closing apparatus." The suborder Conchorhagae possesses a bilaterally divided "closing apparatus" consisting of the first trunk zonite

and retractable placids; suborder Cyclorhagae possesses a cyclic series of from 14 to 16 non-retractable placids which constitute its "closing apparatus" and an undivided ventral plate on the first trunk zonite.

Homalorhage kinorhynchs have been reported from three general world localities—the eastern United States, the southern tip of South America, and Europe. To our knowledge the genus *Pycnophyes*, with thirteen species, is more widely distributed than the genus *Trachydemus*, with only four species.

Methods and Localities

Kinorhynchs were found in samples of the surface layer of mud and detritus collected by an epibenthic dredge from three localities in the San Juan Archipelago. This group of islands is located in the northwest section of the state of Washington between Vancouver Island and the United States mainland. Specific localities and associated collecting data follow.

East Sound, Orcas Island (about lat. 48 degrees 36 minutes N., long. 122 degrees 52 minutes W.), 16 July 1958, mud substrate at a depth of 32 meters.

Echo Bay, Sucia Islands (about lat. 48 degrees 46 minutes N., long. 122 degrees 54 minutes W.), 8 August 1958, mud substrate at a depth of 30 meters.

Reid Harbor, Stuart Island (about lat. 48 degrees 40 minutes N., long. 123 degrees 12 minutes W.), 11 August 1958, mud substrate at a depth of 10 meters.

In the laboratory the samples were placed in white enameled pans and diluted with additional sea water to the consistency of thin soup. As the medium was aerated, kinorhynchs were caught by the minute bubbles of air and brought to the surface, where they became trapped by surface tension and could be removed with a small Irwin loop. Since this material was collected I have found it more efficient to skim off the surface with paper toweling and then, by means of a wash bottle, wash the adhering material into a small dish. This material can be examined under the dissecting microscope for the presence of kinorhynchs.

After the live specimens were studied to note color, et cetera, they were killed and fixed in 70% ethyl alcohol, stained with aceto-carmine, and individually mounted on either microslides or coverslips (the latter method permitted microscopic examination of both dorsal and ventral surfaces). Either Hoyer's or Permount mounting medium was used for these preparations.

Family Pycnophyidae

Genus *Pycnophyes* Zelinka, 1896

Pycnophyes sanjuanensis n. sp. Figs. 1–6

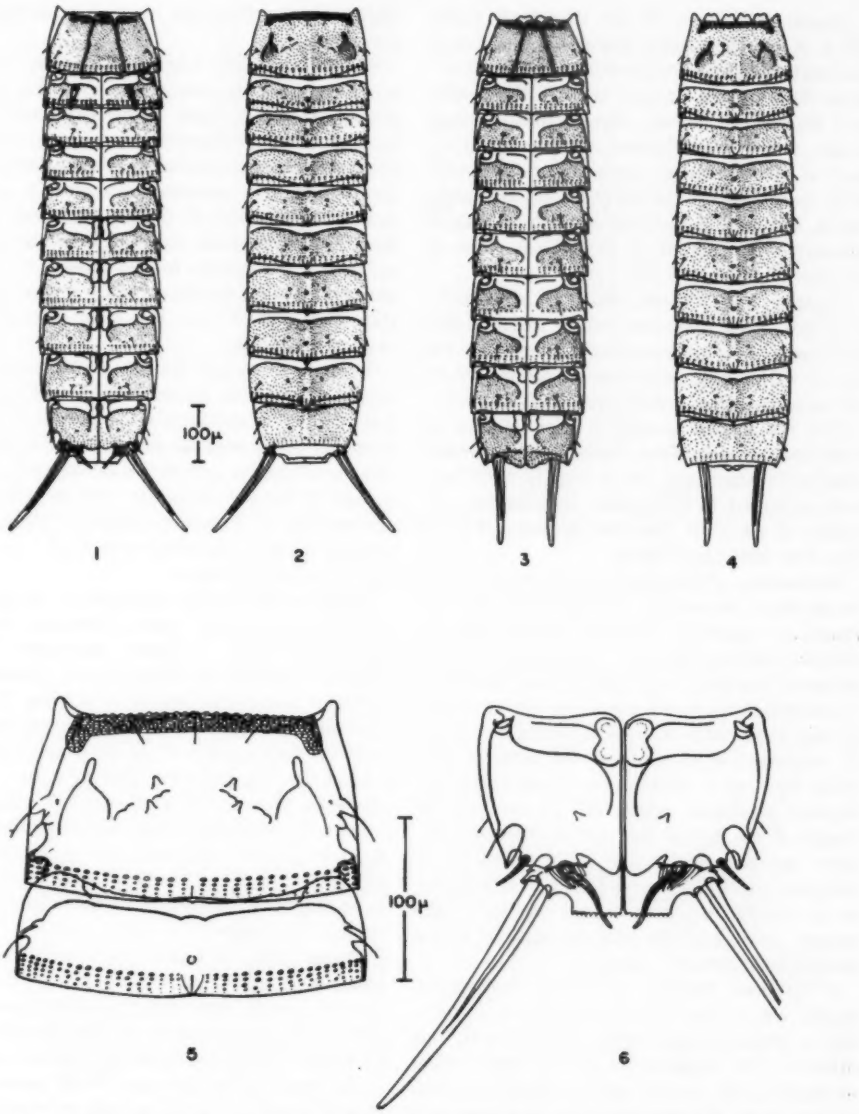
Description. Holotype adult male 826 μ in length (length measurements taken between anterior margin of zonite 3 to posterior margin of zonite 13); maximum width 214 μ; length-width ratio 4.0:1; adult color yellow-brown, pachycycli (thickened anterior margins of the zonites) slightly darker than the remaining portions of the zonites.

Second zonite with four dorsal and two ventral emarginate placids (when retracted, such placids give a "coronate" submarginal appearance to the anterior border of the first trunk zonite); tergal anterior border of zonite 3 distinctively sculptured, shingled or reticulate in appearance; lateral margins of this zonite projecting anteriorly, forming hornlike processes; prominent muscle-attachment zones (thin areas on the zonite) lateral to dorsal midline; dorsolateral and lateral sensory hair present on this zonite; lateral sternal plates with two thin areas along their anterior margin, a ventrolateral sensory hair present on each plate; mid-sternal plate with a single thin area along its anterior border (about one-third of the way posterior there is a slight lateral divergence of the margins of this plate).

Posterior margins of zonites 3 to 12 showing the "Knöpschenreihe" effect, becoming less distinct posteriorly; a weakly developed lanceolate spine present on the posterior mid-dorsal border of zonites 4 to 11, each spine preceded anteriorly by a distinct knoblike structure, probably homologous to the base of a sensory hair; posterior margin of the twelfth tergal plate even, spine lacking; posterior margin of the sternal plates indented slightly near the genital apparatus and then projecting posteriorly near the midline.

Sensory hairs present dorsolaterally, laterally, and ventrolaterally on all trunk zonites except for zonites 5 and 11, which lack lateral sensory hairs; zonite 12, which lacks ventrolateral sensory hairs; and zonite 13, which has no such hairs.

Pachycycli moderately developed; ventral pachycyclus of the fourth zonite bending away



FIGS. 1–6. *Pycnophyes sanjuanensis* n. sp. FIGS. 1, 2. Ventral and dorsal view of adult male (head retracted). FIGS. 3, 4. Ventral and dorsal view of adult female (head not shown, placids everted). FIG. 5. Dorsal view of zonites 3–4 (male). FIG. 6. Ventral view of zonites 12–13 (male). FIGS. 1–4 to same scale. FIGS. 5–6 to same scale.

slightly from the accessory pachycyclus; armor joints of segments 4 to 11 well developed; anteromedial thickenings of the sternal plates well developed on zonites 8 to 12.

Posterior margin of the thirteenth tergal plate distinctly truncate, with three minute spines along the lateral edge of the posterior margin; sternal plates of zonite 13 similarly truncate with minute spines along the entire posterior margin.

Lateral end spines of the thirteenth zonite 193 μ in length, slightly more than one-fourth the length of the trunk; first penis spines short, about 30 μ, located laterally between the twelfth and thirteenth zonites; second penis spines longer, about 50 μ, located anteromedially on each of the thirteenth sternal plates, covered with hairs basally. In addition to the penis spines, the male is distinguishable by a pair of adhesive tubes located on the sternal plates of the fourth zonite.

Allotype, adult female, similar to male, 820 μ in length, 214 μ maximum width; female differs from male in (1) anteromedial thickenings of the sternal plates well developed on zonites 10–12, (2) no penis spines, and (3) no adhesive tubes.

The two known specimens were collected at East Sound, Orcas Island. Both the holotype and allotype (author's nos. K–1.9 and K–1.10) have been deposited in the marine invertebrate collection of the U. S. National Museum (USNM Cat. Nos. 29953 and 29954).

Discussion. *Pycnophyes sanjuanensis* n. sp. bears certain important resemblances to the two European species *P. dentatus* Zelinka and *P. robustus* Zelinka. It has a sculptured anterior margin of the third tergal plate similar to that of *P. dentatus;* none of the remaining twelve species of this genus have such sculpturing. Although *P. sanjuanensis* n. sp. has the same length-width ratio as *P. dentatus*, it differs in size (*P. dentatus* maximum length 700 μ) and relative length of the lateral end spines (between one-sixth and one-seventh the body length in *P. dentatus*). Other differences include the character of the placids, the number and position of the sensory hairs, and the posterior margins of the twelfth and thirteenth zonites.

P. robustus likewise is smaller (maximum length 640 μ) than *P. sanjuanensis* n. sp. and has a similar length-width ratio (3.8:1), but differs in the character of the anterior margin of zonite 3, the number and arrangement of the sensory hairs, the proportion of the lateral end spine length to body length (one-third the body length), and the posterior margins of the twelfth and thirteenth zonites.

Genus *Trachydemus* Zelinka, 1907

Trachydemus ilyocryptus n. sp. Figs. 7–10

Description. Holotype, adult male, 694 μ in length; maximum width 163 μ; length-width ratio 4.3:1; adult color yellow-brown, pachycycli slightly darker than the remaining portions of the zonites.

Second zonite with four dorsal and two ventral emarginate placids; tergal border of this zonite entire, lateral margins projecting anteriorly, forming sharp, elongated, hornlike processes; prominent muscle-attachment zones lateral to the dorsal midline; no sensory hairs present on this zonite; lateral sternal plates thickened anteriorly, the thickened zone gradually becoming constricted toward the medial edge of the plate and ending about two-thirds of the way posterior; thin area present near the anterior border of each sternal plate.

Pachycycli strongly developed; ventral pachycyclus of the fourth zonite sharply bending away from the accessory pachycyclus near the midline; zonites 4 to 12 with armor joints, progressively less developed posteriorly; anteromedial thickenings of the sternal plates well developed on zonites 9 to 12; posterior margins of the twelfth sternal plates projecting posteriorly as they approach the midline.

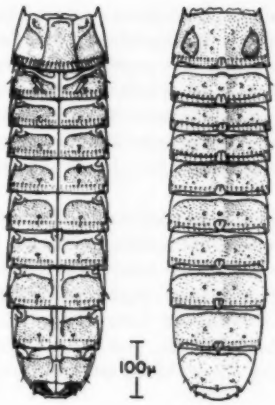
Posterior margins of zonites 3 to 12 showing the "Knöpschenreihe" effect, becoming less distinct posteriorly; a blunt, somewhat "bell-shaped," weakly developed spine present on posterior mid-dorsal border of zonites 3 to 7, becoming broadly lanceolate on zonites 8 to 11, zonite 12 showing only slight evidence of a spine; knoblike structures, some with a sensory hair, preceding the spine on zonites 4, 6, 8, and 10.

Sensory hairs present laterally on zonites 4, 6, 8, 10, and 12; sensory hairs present ventrolaterally on zonites 4 to 11 with a knoblike structure indicating the homologue of a sensory hair ventrolaterally on zonite 12.

Tergal plate of zonite 13 broadly rounded posteriorly, with a lateral terminal club-shaped projection and a more medially located prominent hair on the dorsal border; ventral plates of the thirteenth zonite following the general contour of the tergal plates; first and second penis spines of equal length or nearly so; base of second penis spines covered with hairs; in addition to the penis spines, the male is distinguishable by a pair of adhesive tubes located on the sternal plates of the fourth zonite.

Allotype, adult female, similar to male, 694 μ in length; maximum width 173 μ; length-width ratio 4.4:1; lacking penis spines and adhesive tubes.

The adult males from East Sound were between 612 and 694 μ in length and from 153 to 163 μ



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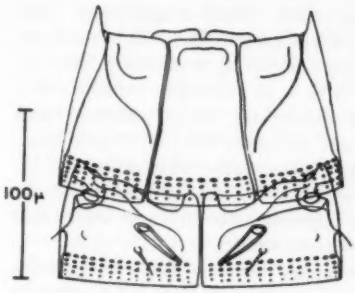

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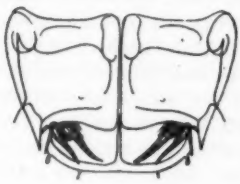

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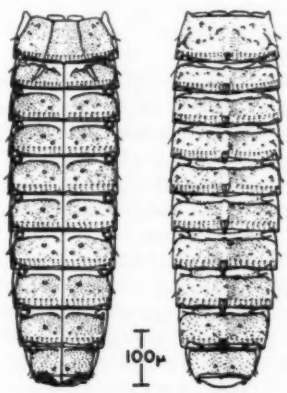

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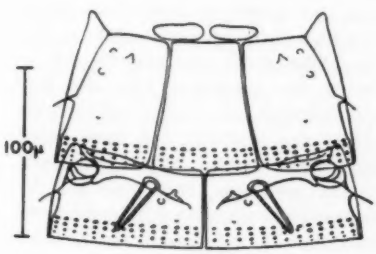

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FIGS. 7–10. *Trachydemus ilyocryptus* n. sp. FIGS. 7, 8. Ventral and dorsal view of adult male (head not shown, placids everted). FIG. 9. Ventral view of zonites 3–4 (male). FIG. 10. Ventral view of zonites 12–13 (male). FIGS. 11–14. *Trachydemus cataphractus* n. sp. FIGS. 11, 12. Ventral and dorsal view of adult male (head not shown, placids everted). FIG. 13. Ventral view of zonites 3–4 (male.) FIG. 14. Ventral view of zonites 12–13 (male.) FIG. 7, 8, 11, and 12 to same scale. FIG. 8, 10, 13, and 14 to same scale.

in maximum width. Their length-width ratio was between 3.8 and 4.3:1. The central tendency of these specimens was approximately 664 μ in length and 163 μ in maximum width. Adult females from this locality were between 664 and 745 μ in length and from 153 to 184 μ in maximum width. Their length-width ratio was between 3.8 and 4.5:1. The central tendency of the females was approximately 694 μ in length and 173 μ in maximum width.

The adult males from Echo Bay were between 633 and 736 μ in length and from 163 to 194 μ in maximum width. Their length-width ratio was between 3.8 and 4.2:1. The central tendency of these specimens was 694 μ in length and 173 μ maximum width. Adult females from this locality were between 664 and 745 μ in length and from 173 to 194 μ in maximum width. Their length-width ratio was between 3.8 and 4.0:1. The central tendency of the females was approximately 725 μ in length and 184 μ maximum width.

No adult males were collected from the Reid Harbor locality and only two females of this species were collected, one 694 μ in length and 184 μ maximum width and the other 745 μ in length and 194 μ maximum width.

In general, the specimens from East Sound were smaller than those from the other two localities. This difference in size may be due to age differences; the specimens from the first locality were collected three weeks before those from the other two localities, and these latter two localities were sampled only a few days apart. The few specimens, both male and female, which were less than 664 μ in length were newly molted adults, as indicated by the development of the exoskeleton. The presence of attached protozoan ectoconsortes on the largest individuals indicated their advanced age.

Type material includes six males and eight females collected at East Sound, Orcas Island; five males and four females collected at Echo Bay, Sucia Islands; and two females collected at Reid Harbor, Stuart Island. The holotype and allotype (author's nos. K–1.55 and K–1.75) have been deposited in the marine invertebrate collection of the U. S. National Museum (USNM Cat. Nos. 29955 and 29956). Two paratypes, one male and one female (author's nos. K–1.42 and K–1.95), have been deposited in the University of Washington Museum; the remaining paratypes are in the author's personal collection. The type locality is East Sound, Orcas Island.

Discussion. *Trachydemus ilyocryptus* n. sp. differs from the four previously described species of this genus by the presence of the peculiarly shaped mid-dorsal spines, the thickened areas on the anterior region of the third lateral sternal plates, the arrangement of the sensory hairs, and the emarginate four-dorsal and two-ventral placids.

Although *T. ilyocryptus* n. sp. is similar to the other species in its length, it appears to have a higher length-width ratio more closely resembling the European *T. giganticus* Zelinka (4.0:1), whereas *T. spinosus* Lang (Lang, 1949), from the Falkland Islands, and the Chilean *T. anomalus* Lang (Lang, 1953) are slightly broader.

Trachydemus cataphractus n. sp. Figs. 11–14

Description. Holotype, adult male, 674 μ in length, 184 μ in maximum width; length-width ratio 3.7:1; adult color yellow-brown, pachycycli slightly darker than the remaining portions of the zonites.

Second zonite provided with four dorsal and two ventral entire placids; tergal anterior border of zonite 3 entire, lateral margins of this zonite project anteriorly, blunt; vague muscle-attachment zones near lateral borders of the tergal plate; sensory hairs present in dorsolateral, lateral, and occasionally ventrolateral positions on the third zonite.

Pachycycli strongly developed; ventral pachycyclus of the fourth zonite bending away from the accessory pachycyclus near the armor joint only; zonites 4 to 12 with armor joints, only slightly less developed posteriorly; anteromedial thickenings of the sternal plates not developed or only slightly evident.

Posterior margins of zonites 3 to 12 showing the "Knöpschenreihe" effect, becoming less distinct posteriorly; lanceolate spines present on posterior mid-dorsal border of zonites 3 to 12, spine on zonite 12 barely evident; posterior margin of zonite 12 not projecting posteriorly.

Sensory hairs present laterally on all trunk zonites except 5 and 11; dorsolateral sensory hairs present on zonites 4 to 11; knoblike structures, rarely with a sensory hair, located dorsally and ventrolaterally as indicated in Figures 11 and 12 (two such structures particularly prominent on the sternal plates of zonites 4 to 11).

Tergal plate of zonite 13 broad, rounded posteriorly, protruding slightly lateroterminally, and variously provided with two or three distinctive spinelike projections and hairs; posterior margin

with minute hairlike projections; sternal plates of zonite 13 following the general contour of the tergal plates; first and second penis spines of equal length or nearly so; base of second penis spine covered with hairs; in addition to the penis spines, the male is distinguishable by a pair of adhesive tubes located on the sternal plates of the fourth zonite.

Allotype, adult female, similar to male, 694 μ in length; 194 μ maximum width; length-width ratio 3.6:1; lacking penis spines and adhesive tubes; zonite 12 small, narrowing rapidly and converging on zonite 13, which appears somewhat reduced.

The adult males from East Sound were between 510 and 612 μ in length and from 143 to 163 μ in maximum width. Their length-width ratio was between 3.3 and 4.0:1. The central tendency of these specimens was approximately 592 μ in length and 153 μ maximum width. Adult females from this locality were between 572 and 654 μ in length and from 153 to 173 μ in maximum width. Their length-width ratio was between 3.5 and 4.1:1. The central tendency of the females was approximately 612 μ in length and 163 μ maximum width.

The adult males from Echo Bay were between 664 and 684 μ in length and from 184 to 194 μ in maximum width. Their length-width ratio was between 3.5 and 3.7:1. The central tendency of these specimens was 674 μ in length and 184 μ maximum width. Adult females from this locality were between 633 and 704 μ in length and from 173 to 204 μ in maximum width. Their length-width ratio was between 3.4 and 3.8:1. The central tendency of the females was approximately 694 μ in length and 194 μ maximum width.

Only two adult males were collected from Reid Harbor—one 633 μ in length and 194 μ maximum width, the other 694 μ in length and 194 μ maximum width. Adult females from this locality were between 654 and 704 μ in length and 194 μ maximum width. Their length-width ratio was between 3.4 and 3.6:1. The mean length for the six specimens was 669 μ.

As with *Trachydemus ilyocryptus* n. sp., the East Sound specimens of *Trachydemus cataphractus* n. sp. generally were smaller than those from the other two localities. Specimens with lengths of less than 528 μ were recognizable as newly molted.

Type material includes 18 males and 24 females collected from East Sound, Orcas Island; 5 males and 8 females collected from Echo Bay, Sucia Islands; and 2 males and 6 females collected from Reid Harbor, Stuart Island. The holotype and allotype (author's nos. K–2.13 and 2.11) have been deposited in the marine invertebrates collection of the U. S. National Museum (USNM Cat. Nos. 29957 and 29958). Two paratypes, one male and one female (author's nos. K–2.15 and K–2.8), have been deposited in the University of Washington Museum; the remaining paratypes are in the author's personal collection. The type locality is Echo Bay, Sucia Islands.

Discussion. *Trachydemus cataphractus* n. sp. agrees with the Chilean species, *T. anomalus* Lang (Lang, 1953) in its general appearance although it lacks the three projections of the third anterior tergal border, differs in the number and arrangement of the lateral sensory hairs, has a differently shaped terminal zonite, and has only two ventral placids instead of four. The relative length of the third zonite is perhaps smaller than the remaining species of this genus; it is otherwise quite distinct.

Summary

Three homalorhage kinorhynchs—*Pycnophyes sanjuanensis* n. sp., *Trachydemus ilyocryptus* n. sp., and *T. cataphractus* n. sp.—are new species of the family Pycnophyidae. All three species, along with *Echinoderes pennaki*, previously described by the author, are found in the San Juan Archipelago, located in the northwest section of the State of Washington between Vancouver Island and the United States mainland.

ACKNOWLEDGMENTS

I am most grateful for the help of Dr. Paul L. Illg and Dr. Dixy Lee Ray of the Department of Zoology, University of Washington, and for the generous manuscript assistance of Dr. C. G. Bookhout and Dr. Joseph R. Bailey, Department of Zoology, Duke University. A grant from the National Science Foundation for summer study at the University of Washington Laboratories, Friday Harbor, Washington, made this work possible.

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Abstracts of Papers Presented at the Fall Meeting of the Society of North Carolina Bacteriologists at Raleigh, N. C., on December 3, 1960

1. **Studies on the Lipopolysaccharide-Free Cell Wall of *Chromobacterium Violaceum*.** *Robert W. Wheat, Duke University Medical Center, Durham, N. C. Chromobacterium violaceum* cells were killed by cold trichloracetic acid or hot ethanol, and lipopolysaccharide-free cell-wall material, equivalent to about 20 per cent of dry-cell weight, was prepared from the acid or alcohol insoluble residue by sequential extraction with 45 and then 90 per cent aqueous phenol. Four fractions were obtained: I, aqueous soluble, phenol insoluble; II, interface; III, phenol soluble; IV, phenol insoluble. The acetone–ether-dried fractions were hydrolyzed 6 hours in 2 NHCl and after removal of HCl, chromatographed on Dowex 50—H^+. Amino sugars were detected by a modified Elson-Morgan colorimetric assay. Better than 95 per cent of the total muramic acid was found in the phenol-insoluble fraction IV, which also contained glucosamine (1 per cent) in roughly equivalent amounts, but no fucosamine. Fucosamine was found in lipopolysaccharide contained in the initial acid extract and aqueous-soluble–phenol-insoluble phase. The phenol-insoluble cell-wall preparations contained all amino acids: twelve which appeared to be present in higher concentrations were alanine, arginine, aspartic acid, diamino pimelic acid, glutamic acid, glycine, the leucines, lysine, serine, threonine, and valine. Deoxyribonucleic acid accounted for from 5 to 13 per cent of these preparations, RNA only 3 to 5 per cent. Little or no heptose was found. Electron micrographs revealed typical cell–wall-like structures.

2. **Virulence of *Pseudomonas Solanacearum* as Influenced by the Proportion of Virulent to Avirulent Cells.** *Charles W. Averre, III, and Arthur Kelman, North Carolina State College, Raleigh, N. C.*

3. **More Specific Response to some Highly Purified Tuberculo-Proteins.** *Javad Vakilzadeh and H. M. Vandiviere, Gravely Sanatorium, Chapel Hill, N. C.* The value of tuberculin as a diagnostic and epidemiologic tool has long been recognized. However, the present tuberculins need improving. Greater sensitivity and specificity is an obvious enigma of import.

Dr. Florence Seibert prepared several purified tuberculo-proteins (designated A, B, C, and Bac. 1). These demanded evaluation in search for an improved antigen.

This study was designed to investigate quantitatively the sensitivity and specificity of these purified fractions. Studies in humans (tuberculous, vaccinated, and healthy naturally sensitized subjects) revealed C protein to be consistently poor; Bac. 1 was erratic. Protein A appeared more sensitive in the immune body. Fraction B seemed more specific and more sensitive than PPD-S in host infected with typical mycobacteria, but had greater sensitivity than A only in active disease.

Another experiment included nine groups of guinea pigs, each sensitized with a different strain of mycobacteria; BCG, Phipps-858; R_1; $H_{37}R_v$; Bovine (Ravenel); Avian (Sheard); killed bovine; and three unclassified (photochromogen, nonphotochromogen, and skotochromogen). Simultaneous skin testing with PPD-S and each fraction was done with periodic regularity. Reactions were carefully measured and analyzed.

The relative differences in host response to fractions observed in the various human categories was verified in the animals.

Animals sensitized with virulent strains of mycobacteria (human and bovine) resulted in like patterns of response (A > PPD-S > Bac. 1; also B > PPD-S > Bac. 1). Both A and B seemed more sensitive than PPD-S. Neither A nor B elicited a response as great as PPD-S in animals injected with avian or unclassified mycobacteria. After challenge, the avian and "atypical" infected animals reacted the same as did the human and bovine infected animals previously.

Thus, a more sensitive and specific tuberculin antigen may be had by obtaining A or B or a combination of both, as each apparently has greater sensitivity and specificity for human bovine infections and less for the avian and nonspecific infections.

A seems to elicit greater response in immunity, whereas B becomes greater in disease.

4. **A Simple, Rapid Method for the Demonstration of Fungi in Clinical Materials.** *Ernest W. Chick, Veterans Administration Hospital, Durham, N. C.*

5. ***In Vitro* Cytotoxicity of Normal Rabbit Serum For Walker 256 Tumor Cells.** *Robert L. Tuttle and J. H. S. Foushee, Bowman Gray School of Medicine, Winston-Salem, N. C.* During the course of studies concerning certain immunologic aspects of the Walker 256 rat tumor, it was found that normal rabbit serum exerted a cytotoxic effect upon suspensions of tumor cells which were being maintained in tissue culture. Substitution of 5 per cent normal rabbit serum for 5 per cent preserved normal horse serum in the growth medium resulted in the failure of the cells to establish a monolayer. Observation of actively growing cells with the phase microscope showed that cytotoxic changes consisting of marked vacuolization and cytoplasmic granularity occurred within 15 minutes after exposure to medium containing 5 per cent normal rabbit serum. Tumor cells which had been incubated at 37°C. for 1 hour in the presence of normal rabbit serum were permeable to trypan blue.

Heating normal rabbit serum at 56°C. for 3 minutes completely abolished the cytotoxic reaction as measured by permeability to trypan blue and viability. Removal of divalent cations by passage through an anion exchange column or the addition of di-sodium ethylenediamine tetraacetate (EDTA) similarly abolished the cytotoxicity of normal rabbit serum. Activity could be restored by the addition of Ca^{++} and Mg^{++}.

Fresh normal human, guinea pig, horse, cat, cow, dog, calf, sheep, chicken, and pigeon serum displayed the same cytotoxic activity. Normal rat and mouse serum were nontoxic.

Normal rabbit serum displayed no activity against KB and HeLa cells. The cytotoxicity of normal rabbit serum could be abolished by absorption with Walker cells but not with KB or HeLa cells.

The heat-lability and divalent cation requirement of the cytotoxic system strongly suggests that the system is complement dependent. Classic immunologic concepts would allow the postulation that a "natural" antibody is involved; however, direct evidence for its presence has not been obtained.

6. **The Long-Chain Fatty Acids of Certain Biotin-Requiring Bacteria.** *Jo Ann Croom and J. J. McNeil, North Carolina State College, Raleigh, N. C.* A study was made of the influence of biotin on the long-chain fatty acids of two biotin-requiring bacteria, *Lactobacillus arabinosus* and a biotin-requiring mutant of *Escherichia coli*. The fatty-acid spectrum of cells grown at a level of biotin permitting half-maximal growth was compared with the spectrum from cells grown at a biotin level giving maximal growth. The fatty acids were extracted and methylated, and the methyl esters were analyzed by gas-liquid chromatography using a succinate-ethylene glycol polyester stationary phase.

L. arabinosus contained six major long-chain fatty acids: myristic, palmitic, stearic, lactobacillic, and unsaturated C_{16} and C_{18} fatty acids. Except for lactobacillic, the *E. coli* mutant contained these same acids, and, in addition, lauric, tridecanoic, pentadecanoic, arachidic, and trace amounts of heptadecanoic. Low biotin concentration depressed the level of the unsaturated acids in *L. arabinosus*, while palmitate increased by a corresponding amount, indicating the participation of biotin in the formation of the unsaturated fatty acids. Fatty acids from the *E. coli* mutant grown at the low biotin level contained more of the unsaturated fatty acids with a decrease in stearate than did cells grown at the high level, almost the opposite effect observed with *L. arabinosus*.

Suggestions to Contributors

Manuscripts for consideration for the Spring issue should be in the hands of the Editor by January 15th, and for the Fall issue by July 20th. They must be typewritten, double-spaced throughout, with footnotes, tables and legends on separate sheets. Since space is limited, papers should be as concise as possible; tables should be reduced to a minimum. Titles should be brief but adequately descriptive of the contents. Each paper should be completely ready for the press, references checked, typographical errors corrected, before its submission to the Editor, at the following address:

DR. WALTER H. WHEELER, *Editor*
Department of Geology and Geography
University of North Carolina
Chapel Hill, N. C.

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In the interest of consistency, authors are strongly urged to conform to the pattern of recent papers *in their field* in this Journal, in arranging headings, citations, etc.

Lists of literature cited follow two distinct styles, a more abbreviated one being allowed in Mathematics and Physics than in other fields, e.g.

(5) BRAUER, A., AND N. MACON. Amer. Jour. Math. **71**: 349–361. 1949.
BAILEY, JOSEPH R., AND DAVID G. FREY. 1951. Darters of the genus *Hololepis* form some natural lakes of North Carolina. Jour. Elisha Mitchell Sci. Soc. **67**: 191–203.
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